# DISPHYLLIDAE AND PHACELLOPHYLLIDAE FROM THE DEVONIAN GARRA FORMATION OF NEW SOUTH WALES

by D. L. STRUSZ

ABSTRACT. As part of a revision of the rugose coral fauna of the Garra Formation of New South Wales, the families Disphyllidae and Phacellophyllidae are studied, particular note being taken of Schouppe's (1958) revision of this group. The arrangement of trabeculae and the dissepimental structure of the two families are discussed.

New taxa described are: Mansuyphyllum bellense sp. nov., M. parvulum sp. nov., M. catombalense sp. nov., Paradisphyllum harnudinetum gen. et sp. nov., and Hexagonaria approximans cribellum subsp. nov., in the family Disphyllidae; Peneckiella boreensis sp. nov., in the family Phacellophyllidae.

Biostratigraphic subdivision of the Garra Formation, a folded and faulted complex of reef and detrital limestones, is not yet possible. It is deduced to be probably Emsian in age, possibly extending to early Couvinian.

THE disphylloid species described in this paper form a significant part of the coral fauna of the Devonian Garra Formation of New South Wales. This formation is a succession of calcareous rocks which crop out in a sixty-mile wide meridional belt; to the north this disappears beneath the margin of the Great Artesian Basin, and southwards it ends near Orange, a city some 120 miles west-north-west from Sydney (see text-fig. 1). This belt of outcrops of the Garra Formation, up to five miles wide, is recognized as marking an area of relatively shallow water (the Molong Geanticline) throughout most of the early Palaeozoic history of the Lachlan Geosyncline, as Packham (1960) has called this part of the Tasman Geosyncline.

#### STRATIGRAPHY

Overlying the Garra Formation are sandstones of the Late Devonian Catombal Group, recently described by Conolly (1963). The junction between the two is in some places disconformable, in others gently unconformable. Beneath the formation is a succession of volcanic rocks and sediments, ranging in age down into the Silurian. This boundary, on the present available evidence, appears to be conformable over much, if not all, of the western side of the Molong Geanticline, but on its eastern side the situation is confused by strike faulting, and the relationship to the underlying beds is obscure, possibly unconformable.

Sedimentation apparently ceased after deposition of the Catombal Group, and the region was then folded about en echelon meridional axis, probably in the early Carboniferous.

Essentially, the Garra Formation consists of some 3,000 to 4,000 feet of deposits formed in and around an area of reef development. Consequently, these deposits show highly complex horizontal and vertical relationships. The two dominant lithologies are calcareous shale and detrital limestones. These are interspersed with reef-type deposits, which range from two or three rather large bioherms down to thin biostromes built by

[Palaeontology, Vol. 8, Part 3, 1965, pp. 518-71, pls. 72-78.]

laminar stromatoporoids. The detrital limestones include all types, but are predominantly fossiliferous calcarenites, which are frequently thinly interbedded with calcareous to non-calcareous shale. In some areas there are extensive outcrops of algal limestones and pellet or oolite calcarenites; these are generally only sparsely fossiliferous.

It has, unfortunately, not yet proved possible to subdivide the Garra Formation, and so no attempt can be made to assign the various species to precise stratigraphic levels. In a few cases only, it may be possible to state that a particular outcrop is near the top or bottom of the formation. This lack of subdivision follows from the interaction of a number of factors. Firstly, it was found that the rock types vary rapidly both laterally and vertically—a natural consequence of the environment of deposition. However, individual horizons could not be traced for any great distance along the strike, because of highly sporadic outcrop. In many areas the sporadic outcrops are confined to creeks and gullies, and the gaps in outcrop (often occupied by wheat-fields) may be as much as four miles. Further, it was found that there is considerable tectonic disturbance, consisting of strong folding, with close drag-folding in the less competent strata, and frequent strike faulting of variable and often uncertain extent.

The result is that correlation of outcrops is hazardous, even at times over distances (along the strike) of as little as a quarter of a mile. Certainly no detailed stratigraphic

or faunal correlation can at present be attempted for the Garra Formation.

Further descriptions of the geology of the region may be found in: Joplin and Culey (1938), Basnett and Colditz (1946), Joplin and others (1952), Conolly (1963), and Strusz (1963, 1964, 1965).

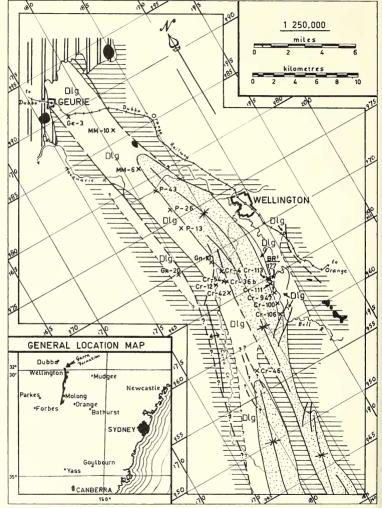
#### AGE OF THE FAUNA

Hill (1942c) recognized two distinct coral faunas, one ('Garra') early Devonian and the other ('Murrumbidgee') early Middle Devonian in age. The much more extensive collections made during this study show that this simple division is probably not tenable, since all the species which characterize the 'Garra' fauna, with the possible exception of *Radiophyllum arborescens* (Hill and Jones 1940), appear to extend from the bottom to the top of the formation, and many of the 'Murrumbidgee' species either do likewise, or are confined to a large biostrome near the top of the formation as preserved in the Wellington district.

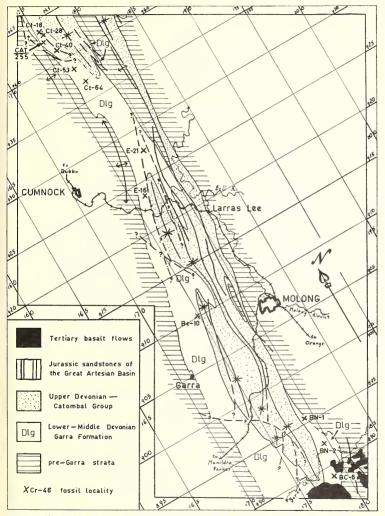
The eastern Australian coral fauna with which the Garra fauna (as now known) may be most readily compared is that from the Murrumbidgee River area of New South Wales (Hill 1940b). This has generally been regarded as equivalent to the Couvinian Stage, but Pedder (1964, p. 365) considers it '. . . more likely to be Siegenian'—without stating reasons for this suggestion. This Murrumbidgee fauna in turn is very similar to the Buchan Limestone fauna of Victoria; a third of the Murrumbidgee species is known from Buchan, and over 40 per cent. of the Buchan species occur in the Murrumbidgee limestones. On the basis of goniatites, Teichert (1948) placed the Buchan Limestone in the Lower Couvinian, but Erben supports a Lower Devonian age.

Garra species also known from overseas faunas are: Pseudochonophyllum pseudohelianthoides (Sherzer)—Siegenian of Czechoslovakia; Rhizophyllum enorme Etheridge fil.—Coblenzian, Kuznetsk Basin (Bulvanker 1958); Spongophyllum halysitoides Eth. fil. —Lower Couvinian, Kuznetsk Basin; probably Xystriphyllum dunstani (Eth. fil.)—

Couvinian, Kuznetsk Basin.



TEXT-FIG. 1a. Geological map of the Wellington region, showing positions of localities listed in the text. Inset: general location map, central and eastern N.S.W.



TEXT-FIG. 1b. Geological map of the Molong region, showing positions of localities listed in the text.

From the foregoing, I consider that the Garra Formation is probably equivalent in age to the Emsian; it may range up into the early Couvinian, or possibly down into the Siegenian.

#### PREVIOUS TAXONOMIC WORK

The first corals to be described from the Garra Formation were those of Etheridge Jr. (1895b, 1898, and 1903). His final contribution was in the 1907 monograph on Australian species of *Tryplasma*. More recent and extensive descriptions of Tabulata and Rugosa are in the series of papers by Hill (1942c), Hill and Jones (1940), Jones (1936, 1944), and Jones and Hill (1940). Finally, Packham (1954) described a *Hadrophyllum* from Curra Creek, near Wellington. All of these papers were based on rather limited collections, representing less than half the outcrop area of the Garra Formation. The extensive collections made in the course of this study (over 6,000 specimens) include many new forms, which will be described in this and subsequent papers.

The following species are described:

Family Disphyllidae Hill 1939: Mansuyphyllum bellense sp. nov., M. parvulum sp. nov., M. catombalense sp. nov., M. catombalense subsp. nov.?, M. sp. A, M? sp. B, M. sp. C, Zelolasma gemmiforme (Etheridge fil. 1902), Disphyllum sp. cf. gregorii (Etheridge fil. 1892), Paradisphyllum harundinetum gen. et sp. nov., Hexagonaria approximans cribellum subsp. nov., Billingsastraea aperta (Hill 1942), B. speciosa (Chapman 1914).

Family Phacellophyllidae Wedekind 1922: *Peneckiella mesa* (Hill 1942), *P. boreensis* sp. nov., *P.* sp. cf. *minor kunthi* (Dames), *sensu* Różkowska 1960, *Phillipsastrea oculoides* Hill 1942.

Abbreviations. The following abbreviations are used in both the text and illustrations:

- Dc Corallite diameter; for solitary and fasciculate corals, the mean diameter measured in a horizontal transverse section, or the minimum diameter measured in an oblique transverse section. For cerioid corals, the maximum diagonal measured in a horizontal transverse section.
- Dt Tabularium diameter.
- R Corallite radius—used when expressing the relative width of concentric structures such as the dissepimentarium, or the relative length of septa.
- Ts Tabularial spacing: the distance between the axes of neighbouring tabularia in astraeoid, thamnastraeoid or aphroid corals, where it is frequently not possible to measure Dc.
- *n* Number of septa (of both orders); n/2 is the number of major septa.
- $L_1$  Length of major septa.
- Lo Length of minor septa.

The repositories of type and other specimens are indicated by the following prefixes to their catalogue numbers:

- AM thin-section numbers, Australian Museum, Sydney, N.S.W.
- AM F fossil numbers, Australian Museum.
- GSQ Geological Survey of Queensland.
- GSV Geological Survey of Victoria.
- NM National Museum, Melbourne, Victoria.
- SU University of Sydney Palaeontological Collection; Sydney, N.S.W.
- UOF University of Queensland Palaeontological Collection; Brisbane, Queensland.

#### SYSTEMATIC PALAEONTOLOGY

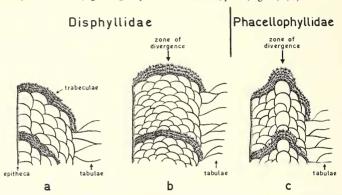
Subdivision of the disphylloid rugose corals into family-group taxa is still very unstable. Classifications range from that of Lecompte (in Piveteau 1952, p. 470), with all the disphylloid genera placed in the one family Disphyllidae, to the classification of Soshkina (1952 et seg.), with families Thamnophyllidae, Peneckiellidae, and Neocampophyllidae. The generally accepted grouping is into two (either families, or subfamilies of the one family) characterized essentially by the presence or absence of a vertical series of horseshoe-shaped dissepiments. This is the grouping found in the Treatise on Invertebrate Paleontology (Hill in Moore 1956); subfamilies Phacellophyllinae and Phillipsastraeinae respectively. Wang (1950) proposed a similar subdivision, but based on the arrangement of the septal trabeculae into 'fans'. The two classifications differ in the detailed grouping of genera, because the two closely related features of dissepimental and trabecular arrangement were not considered in close conjunction by Wang.

In this paper, the genera are grouped into the two families Disphyllidae Hill, and Phacellophyllidae Wedekind. Just how closely related these families are is still a matter for discussion. In both, the septa are composed of slender trabeculae, which in tangential sections through dilated portions are seen to diverge symmetrically from the median plane of the septum. The dissepimentarium is well developed, generally consisting of several series of globose interseptal vesicles. The structure of the tabularium is variable, and frequently complex. The principal distinction lies in the presence (Phacellophyllidae) or absence (Disphyllidae) of horseshoe dissepiments, and in the consequent arrangement of the trabeculae; for in all cases, the trabeculae grow at right angles to the surface formed by the dissepiments at any given stage of growth (see textfig. 2).

In the Disphyllidae, the most common arrangement is that shown by many species of Hexagonaria Gürich. The dissepiments are small, numerous, and globose; peripherally they are horizontal or gently axially inclined, and this inclination increases steadily towards the tabularium. In some species, the dissepiments forming the inner margin of the dissepimentarium are vertical. Consequently, the septal trabeculae are vertical or only slightly axially directed near the epitheca, and towards the tabularium become increasingly axially directed, that is, they are inclined upwards and inwards towards the axis at an angle from the vertical which increases as the axis is approached. The resulting trabecular arrangement may be termed a 'half-fan'. See text-fig. 2a.

A less common alternative arrangement is met with particularly in massive colonial species, but has not as yet been used to distinguish genera. The dissepiments are essentially grouped into three merging concentric zones. In the middle zone they are horizontal, while in the other two zones they are inclined away from this middle zone, the inclination increasing with distance. The calix in these species therefore has a broadly reflexed rim surrounding the axial pit. The trabeculae, reflecting this arrangement, are vertical in the middle zone, and diverge from this zone at ever-increasing angles towards both periphery and axis, so forming full 'trabecular fans'. These fans may or may not be symmetrical about the zone of divergence. See text-fig. 2b.

'Trabecular fans' are also present in the Phacellophyllidae—indeed are characteristic of the family. However, in this case the zone of divergence of the fans corresponds exactly to a vertical series of horseshoe-shaped dissepiments (text-fig. 2c), and it is this combination of features which distinguishes the family from those Disphyllidae with trabecular fans. A further result of this feature is that in those genera in which the horseshoe series is separated from the epitheca by one or more series of normal dissepiments, the calix has a strongly reflexed rim, frequently with a concentric ridge immediately outside the axial pit. This condition is extreme in *Macgeea*, in which the outer edges of the septa are not covered by epithecal deposits for a considerable distance below the distal extremity of the calice (e.g. *Macgeea proteus* Smith 1945, pl. 24, figs. 2, 3, 5).



TEXT-FIG. 2. Arrangement of the dissepiments and trabeculae in the Disphyllidae (a—'half-fans', b—'disphylloid fans') and the Phacellophyllidae (c—'phacellophylloid fans'); diagrammatic longitudinal sections, about  $\times$  2.

To distinguish them, the two types of trabecular fan are herein termed 'disphylloid fans' (without horseshoe dissepiments), and 'phacellophylloid fans' (with horseshoes).

It should be noted that, contrary to various statements (e.g. Różkowska 1953, p. 7), the trabecular fans are not always completely symmetrical about the horseshoe series. It is only in the immediate vicinity of this series that the trabeculae are symmetrically disposed. See for example *M. berdensis* Soshkina of Różkowska (1953, pl. IV, fig. 10).

Apart from the problems of classification outlined above, there is also a difficult nomenclatural problem associated with this group of corals. The earliest family-group name used was Phillipsastraeidae, by C. F. Römer (1883), with the nominal type-genus *Phillipsastrea* d'Orbigny 1849. The family concept attached to this name corresponds to the Disphyllidae as used herein. However, it has recently been shown (see Schouppé 1958) that the type species of *Phillipsastrea*, *P. heunahi* (Lonsdale 1840), possesses a series of horseshoe dissepiments surrounding the tabularium. Consequently this genus must be grouped with the Phacellophyllidae, and takes precedence as nominal type-genus for that group. This move would obviously cause some confusion of the generally accepted concepts attached to the resulting family-group names; this is therefore a case which should be submitted to the International Commission on Zoological Nomenclature for a decision.

# Family DISPHYLLIDAE Hill 1939 Genus MANSUYPHYLLUM Fontaine 1961

Type species. Cyathophyllum annamiticum Mansuy, 1913, p. 9, pl. 1, fig. 11, pl. 2, fig. 12.

Diagnosis. 'Corallites solitary, ceratoid, with cup-shaped calix. Septa of two orders, often bearing weak carinae, continuous as far as the wall. The major septa extend almost to the axis. The minor septa are as long as, or slightly longer than, half the radius. The wide dissepimentarium consists of small globular vesicles; these, right at the periphery, are horizontal; towards the interior, convex and slightly inclined towards the axis, they decrease in size. The relatively narrow tabularium is divided into two series: an axial series where the tabulae are generally complete, horizontal; a periaxial series where they form large vesicles contrasting with the small vesicles of the dissepimentarium.' (Translated from Fontaine 1961, p. 100.)

Discussion. Fontaine erected this genus to contain solitary disphyllids with the internal structure of Disphyllum. He distinguished it from Breviphyllum Stumm 1949, by its biseriate tabularium and wide dissepimentarium. Moreover, Breviphyllum has amplexoid septa, and when these are dilated (which is rare) the dilatation occurs at the periphery, or is rhopaloid. In the type species of Mansuyphyllum, and in other species assigned to the genus, dilatation is spindlewise when present.

Mictophyllum Lang and Smith 1935, differs in that the minor septa are absent or poorly developed; also the tabularium is generally composed of numerous tabellae which are not clearly arranged in two series.

Species placed in *Mansuvphyllum* by Fontaine are:

Cyathophyllum annamiticum Mansuy 1913: type species.

Campophyllum soetenicum Schlüter, of Soshkina 1952, pl. 23, fig. 86.

Campophyllum boreale Soshkina 1951; Soshkina 1952, pl. 23, fig. 85. Soshkina (1952) stated that this species is colonial; it is therefore probably not Mansuvphyllum.

Campophyllum litvinovitshae Soshkina 1949; Soshkina 1952, pl. 23, fig. 87. As figured by Soshkina (1952), this species differs from Mansuphyllum annamiticum in having a tabularium composed of sagging, generally complete tabulae, with no periaxial zone of tabellae; it seems to be closer to Breviphyllum Stumm.

Campophyllum crassoseptatum Yoh 1937, pl. 7, figs. 5-6.

Disphyllum (or Macgeea) trochoides Hill 1942a, pl. 8, figs. 5-10.

Disphyllum (or Macgeea) excavatum Hill 1942a, pl. 8, figs. 11-13.

Fontaine also considered that Tabulophyllum cylindricum Sun 1958, T. curvatum Sun, and T. gigantum Sun probably are species of Mansuyphyllum. Finally, he considered that two very poorly described species of Sinodisphyllum Sun, described as colonial but in the figures apparently solitary, may be Mansuyphyllum; in this case Sinodisphyllum would be the senior synonym. However, Fontaine considered that Sinodisphyllum at present is unusable because of the poor description. I have not seen the paper in question, so for the present accept Fontaine's conclusions.

I consider that the Australian species of *Mictophyllum*, which differ from the Canadian species (particularly the type species) in having fairly well developed minor septa, are probably best placed in *Mansuyphyllum*. So also is *Mictophyllum richardsoni* (Meek) of Smith (1945, pl. 5, figs. 10–12), from the Canadian Middle Devonian, which Smith only

tentatively assigned to *Mictophyllum*. The Australian species which are most like *Mansuyphyllum* are:

Mictophyllum trochoides Hill 1940b, pl. 11, figs. 7–10. Mictophyllum cf. cresswelli (Chapman) of Hill 1942b, pl. 3, fig. 9. Mictophyllum aff. cresswelli (Chapman) of Philip 1962, pl. 23, figs. 3, 4.

Hill (1954) has noted that *Mictophyllum cresswelli* appears to be weakly colonial, in which case it would not be *Mansuyphyllum* as strictly defined. *M. cresswelli* var. *cylindricum* Hill 1954, does not have a biseriate tabularium. All the Australian species of *Mictophyllum* require further study.

Mansuyphyllum bellense sp. nov.

Plate 72, figs. 1-3; text-fig. 7e

Holotype. SU 11295 (Pl. 72, fig. 1), loc. Be–10. Other material figured: SU 20099, 12110, both loc. Be–10. Derivation of name. From the parish of Bell, in which is situated the type locality.

Diagnosis. Large Mansuyphyllum with fusiform septa, counter and cardinal longer than others; inner part of tabularium composed of small globose tabellae arranged in broad domes; peripheral dissepiments inclined outwards.

Description. The external characteristics are poorly known, as all available specimens are badly worn. The corallite is apparently trochoid, reaching a diameter of over 2.5 cm. The calix is apparently shallow, with a broad reflexed rim, and a broadly domed floor to the axial pit.

Dimensions in mm. (representative specimens):

	Dc	Dt	Dt/Dc	n
SU 11295	> 30.5	16.0	< 0.53	c. 70-80
SU 12109	> 26.0	13.5	< 0.52	64
SU 12110	> 23.0	11.0	< 0.48	64

All the specimens are worn, so the measured values of Dc are less than the true values, and calculated values of Dt/Dc are inflated accordingly. This is shown here and in subsequent tables by the use of the signs > and <.

There are over sixty septa. The long major septa leave an axial space only 3 mm. across, into which project the counter and cardinal septa. These generally intertwine at the axis, and frequently one or both extend nearly to the opposite side of the axial space. The remaining major septa frequently are pinnate about the counter-cardinal plane. The minor septa, about half as long as the major, terminate at the margin of the tabularium.

In the dissepimentarium both orders of septa are straight and fusiform, the major septa being more strongly dilated than the minor. Rare irregular carinae may occur outside the zone of dilatation. The ends of the counter and cardinal septa are generally slightly dilated.

The trabeculae are very slender, arranged in wide disphylloid fans. The zone of divergence of the fans is near the periphery; outside this zone, the trabeculae are moderately inclined outwards; inside the zone they are increasingly axially inclined, until

they are about 70–80° from the vertical at the margin of the tabularium. In the tabularium they curve upwards once more.

The biseriate tabularium consists of a very wide axial zone in which the tabular floors are domed, surrounded by a narrow trench-like periaxial zone. The axial zone is composed of numerous small, fairly globose tabellae, while the periaxial zone is made up of a series of flat or sagging tabellae, which tends to be vertically discontinuous. Consequently, the outermost axial tabellae often interleave with the innermost dissepiments, the only difference then being in the direction of inclination.

The dissepimentarium generally equals  $\frac{1}{2}$  R, and is composed of 9–14 series of small globose dissepiments. These diverge quite markedly from a zone near the periphery, so dividing the dissepimentarium into three zones. The outer zone is of 2–3 series of dissepiments which are moderately to strongly inclined outwards; the middle zone is of or 2 series of globose horizontal plates; and the inner zone is of 6–9 series of strongly axially inclined plates.

Comparison. M. bellense is close to the type species in size and number of septa (50–60 in M. annamiticum), and also in having a wide dissepimentarium. The major differences are in the arrangement of the tabellae, and in the strongly fusiform septa in M. bellense. Another point of difference is in the marked elongation of the counter and cardinal septa—a character lacking in all described species assigned to Mansuyphyllum, but which is found in a number of Garra disphyllid species.

Known localities. Be-10 (common), Cr-4.

Mansuyphyllum parvulum sp. nov.

Plate 72, figs. 4-6; Plate 73, fig. 1; text-figs. 3, 7 a, b

Holotype. SU 14224 (Pl. 72, fig. 6, Pl. 73, fig. 1), loc. Ct–40. Other material figured: SU 14223 (loc. Ct–40), 18151 (loc. CAT/255).

Derivation of name. Latin parvulus, very small.

*Diagnosis*. Diminutive *Mansuyphyllum* with numerous fusiform septa; calix deep, with everted rim.

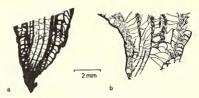
Description. Solitary turbinate to trochoid corallites, whose maximum diameter is about 10 mm. The epitheca is moderately rugate, and bears shallow, irregular septal grooves. There are also irregular lateral talons. The calix is wide and deep, with a flat or slightly domed floor, and a rather wide everted rim; the major septa project above the floor and walls of the calix.

Dimensions in mm.

Specimen	Loc.	Dc	Dt	Dt/Dc	11
SU 12296	Cr-36b	> 6.0	4.0	< 0.6	52
,,	,,	8.8	5.5?	0.6?	> 32*
SU 14223	Ct-40	5.2	3.0	0.58	38
SU 14224	**	8.8	c. 4·5	c. 0·5	48
,,	,,	10.1			> 38*
SU 18152	CAT/255	7.5	4.5	0.6	52

<sup>\*</sup> Calical section.

Adult corallites have about 48–52 septa. Serial transverse peels of SU 18151 show that the septa are inserted quite rapidly: at Dc = 5.9 mm., n = 46; at 8 mm., n = 50, and at 9.5 mm. (the base of the calice) n = 50 still. The first section is from about half-way between the apece of the corallite and the base of the calix. The septa are strongly fusiform, with the major the more strongly dilated; they attenuate rapidly within the tabularium. The major septa are long, more than  $\frac{2}{3}R$ ; one, probably the counter septum, extends into the axial space (which is 1.5-2 mm. across), and may reach its opposite side. The other septa may be slightly pinnate about the counter-cardinal plane. The minor septa equal  $\frac{1}{3}-\frac{1}{2}R$ , ending at the margin of the tabularium. Towards the periphery there are poorly developed irregular carinae, while in at least one transverse section there are short discontinuities in the septa about the margin of the tabularium.



TEXT-FIG. 3. Mansupphyllum parvulum sp. nov. Longitudinal sections, × 5. a, Holotype SU 14224 (loc. Ct-40), traced from photograph of celluloid 'peel' (Pl. 72, fig. 6). b, SU 18151 (loc. CAT/255), traced from photograph (Pl. 72, fig. 5).

The slender trabeculae are curved, arranged in disphylloid fans. Those at the periphery are directed only slightly outwards, while those at the margin of the tabularium are directed axially at about 30° from the vertical.

The tabularium is irregularly biseriate; the wide axial series consists of flatly domed complete and incomplete tabulae, while the narrow periaxial series consists of small, flat to inclined tabellae. The outer margins of the axial series are often supplemented by globose vesicular tabellae.

There are three to four series of dissepiments (more in the extensions of dissepimental tissue into the larger talons). These are irregular in size, generally strongly globose. The innermost series is moderately to strongly axially inclined, and the others are horizontal to slightly peripherally inclined. The inner one or two series are generally strongly invested with fibrous septal tissue.

Comparison. M. parvulum differs from all previously described species in its small size. It differs from the type species in having a slightly reflexed calical rim. Very similar in size and structure is M. catombalense sp. nov., described hereunder. For detailed comparison, see p. 530.

Remarks. This species at first seems close to Kunthia Schlüter 1885, with its deep calix and fusiform septa (see Stumm 1949, pl. 12, figs. 22–23). However, in that genus the calix reaches almost to the apex of the corallite, which is not the case in M. parvulum. As

the type, K. crateriformis, is poorly known, further comparison must await its reexamination.

Known localities. Cr-36b, Ct-40 (type), P-13, CAT/255.

Mansuyphyllum catombalense sp. nov.

Plate 73, figs. 2 a-c; text-figs. 4, 7d

*Holotype*. SU 14155 (Pl. 73, figs. 2*a*–*c*); paratype. SU 14156, both from loc. Ct–18.

Derivation of name. From the parish of Catombal, in which occurs the type locality.

*Diagnosis.* Small *Mansuyphyllum* with narrow dissepimentarium; minor septa often discontinuous; counter septum extends across narrow axial space.

Description. This species is known only from thin sections, and so the external features are poorly known. Corallites are ceratoid, with marked growth irregularities, and talons are developed for lateral attachment. Adult corallites near the mode are 7 or 8 mm. in diameter; the maximum known is 10 mm. The calix has a narrow rounded rim, a steeply sloping wall, and a wide floor containing a broad, low, flat-topped axial boss.

Dimensions in mm.

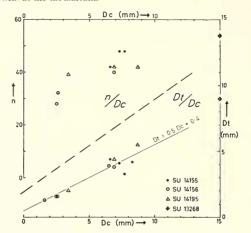
Specimen	Dc	Dt	Dt/Dc	n	$L_1$	$L_2$	Axial space
SU 14155	7.3	3.4	0.47	48	0.9 R	0.6 R	0.8
,,	9.6	4.0	0.42	44	0.8 R	0.5 R	1.0
,,	7.5	3.9	0.52	48	0.9 R	0.4 R	1.0
SU 14156	7.0	3.4	0.49	40	0.9 R	0.6 R	0.9

There are 40-48 septa in adults. The major are long (0.8-0.9 R), leaving an axial space about 1.0 mm, wide. The counter septum extends across this space, almost meeting the cardinal septum; it may be slightly dilated, or turned aside, but there is no definite columella. The counter-lateral septa are a little withdrawn, and the remaining septa are pinnately arranged about the counter-cardinal plane. The minor septa equal about R, and terminate just inside the tabularium. Septal dilatation is fusiform, and moderate to very strong. In a zone about 0.5 mm, wide around the tabularium the septa are frequently dilated so as to come into contact; outside this zone they may, rarely, retain this strong dilatation to the periphery, but are normally only moderately dilated. In the dissepimentarium the septa may be straight and smooth, or zigzag, or irregularly carinate. In the tabularium the septa are usually straight, and only rarely bear poorly developed carinae. The minor septa are generally discontinuous in the outer part of the dissepimentarium, and may be so throughout their length, at times to the extent of occurring as a series of detached trabeculae. In only one section are there peripherally discontinuous major septa, and these are in a portion of the corallite immediately below a sudden growth constriction.

The trabeculae are monacanthine and thick—up to 0.5 mm. in dilated portions of the septa; there is only one radial series in each septum. At the periphery they are vertical or slightly axially inclined; this inclination from the vertical increases steadily inwards, so that the individual trabeculae are curved. The inclination is about 60° from vertical at the margin of the tabularium. Within the tabularium the inclination appears to decrease, the trabeculae being generally directed sharply upwards.

The wide tabularium is biseriate. The axial series consists of wide, flat-topped domes. The periaxial series consists of peripherally inclined tabellae. The margins of the axial series are in places supplemented by small globose tabellae. A plot of Dt against Dc shows that this ratio remains constant during growth (text-fig. 4). The growth equation is: Dt = 0.5 Dc + 0.4.

The narrow dissepimentarium, about  $\frac{1}{3}$  R, is made up of one to five series of small globose dissepiments; these are horizontal at the periphery, increasing to steeply inclined or vertical at the tabularium.



TEXT-FIG. 4. Plots of *n* against *Dc* (above) and *Dt* against *Dc* (below) for *Mansuyphyllum catombalense* sp. nov. and subsp. nov?

Comparison. A very similar species is M. parvulum sp. nov. Both are small, with fusiform septa and an elongate counter septum. They have similar biseriate tabularia, and not very dissimilar dissepimentaria. The differences are:

- Mansuyphyllum parvulum is turbinate to trochoid; Mansuyphyllum catombalense is ceratoid.
- (2) Mansuyphyllum parvulum has an axial space of about 1·5-2·0 mm. In Mansuyphyllum catombalense it is 1·0 mm. or less.
- (3) The minor septa in Mansuyphyllum parvulum are very rarely discontinuous; in Mansuyphyllum catombalense they are generally so, as also at times are the major septa.
- (4) Unlike Mansuyphyllum parvulum, in Mansuyphyllum catombalense the septa may remain strongly dilated outwards from the zone of maximum dilatation.
- (5) In Mansuyphyllum parvulum, Dt/Dc is about 0·5-0·6, in Mansuyphyllum catombalense about 0·4-0·5.

It is nevertheless clear that the two species are quite closely related. *M. parvulum* is known from calcarenites or silty calcarenites, while *M. catombalense* is known only from two localities in a crinoid–coral biostrome. It is therefore highly likely that the two species have become differentiated by adaptation to the two distinct environments. See also p. 540.

Known localities. Ct-18 (type), Ct-28.

Mansuyphyllum catombalense subsp. nov?

Plate 72, figs. 8 a, b; text-fig. 7f

Material. Transverse and longitudinal sections, SU 13268 from loc. Cr-100.

Description. The only known corallite is worn, but is apparently solitary and ceratoid. It is at least 15 mm. in diameter. Calix and epitheca are unknown.

There are fifty-four septa, showing a marked fusiform dilatation at the margin of the dissepimentarium; the major are considerably more dilated than the minor. The pinnate arrangement of the septa is more marked than in *M. catombalense* s.s., and both the counter and cardinal septa extend into the oval axial space, almost meeting at its centre. The trabeculae do not appear to be arranged in a disphylloid fan system. They are rather wavy, and axially directed at about 60° from the vertical. The tabularium is not well known, but appears to be biseriate, with a periaxial series of globose tabellae supplementing an axial series of flat to domed tabulae. The dissepimentarium is wide, composed of at least nine series of small, globose, strongly inclined dissepiments.

Comparison. This specimen differs from M. catombalense s.s. essentially in its greater size and number of septa, and in having a relatively wider dissepimentarium with considerably more series of dissepiments. The fusiform dilatation of the septa around the tabularium is also more abrupt.

Remarks. The limited material does not warrant naming, but it seems likely that this is a subspecies of *M. catombalense* which has differentiated in response to a change of environment. The latter species has been found only in a crinoidal biostrome, while SU 13268 is from a large coral biostrome near Wellington, which appears to have been a rather quieter environment, associated with deposits of pellet calcarenites and algal limestones. See also text-fig. 7.

# Mansuyphyllum sp. A

Plate 72, figs. 9 a, b; text-fig. 7c

Material. SU 20101 (Pl. 72, figs. 9 a, b), loc. Be-10; SU 12250, loc. Cr-4.

Description. As the only material consists of thin sections, the precise external features are unknown. There appear to be some transverse growth irregularities, but septal grooves are only intermittently developed. The calix is unknown. Adult corallites are about 9 mm, in diameter.

Dimensions in mm

Specimen	Dc	Dt	Dt/Dc	n	$L_1$	$L_2$
SU 20101	8.6	4.7	0.55	50	c. R	$\frac{1}{2}R$
,,	5.4	2.9	0.54	36	,,	,,
SU 12250	9.6	4.8	0.50	50	**	,

The epitheca is thin, and is lined internally by lamellar tissue no more than 0·2 mm. thick. In adults, n=40–50. The major septa are long, leaving an axial space  $1\cdot0\times0\cdot6$  mm.; their ends are pinnately arranged about the counter-cardinal plane. The counterseptum crosses the axial space to unite with the end of the cardinal septum. The counterlateral septa are a little withdrawn, and in the smallest of the available transverse sections the minor septa between them and the counter septum are nearly as long as the major septa. The other minor septa are about  $\frac{1}{2}R$ , barely entering the tabularium. Septal dilatation is very strongly fusiform, and at the margin of the tabularium spreads over the innermost dissepimental surfaces in the very narrow interseptal loculi, to form a stereozone up to 1 mm. wide. In the dissepimentarium the thinner parts of the septa develop irregular carinae.

The trabeculae are arranged in typical disphylloid half-fans. Vertical or slightly inwardly directed at the periphery, their inclination increases axially until within the tabularium they are inclined inwards at about  $60^{\circ}$  from the vertical. The tabularium is a little over  $\frac{1}{2}$  Dc; only one fragmentary longitudinal section is available, and in this the tabulae are apparently incomplete, globose, and possibly arranged in two series, the axial ones being flatter than those near the dissepimentarium. The narrow dissepimentarium is composed of some four or five series of small, highly globose vesicles. These are horizontal at the periphery, becoming very steeply inclined at the margin of the tabularium. The dissepiments also decrease in size axially.

Comparison. These two specimens appear to be about half-way between M. parvulum and M. catombalense. For a detailed comparison see table, p. 541.

Mansuyphyllum? sp. B

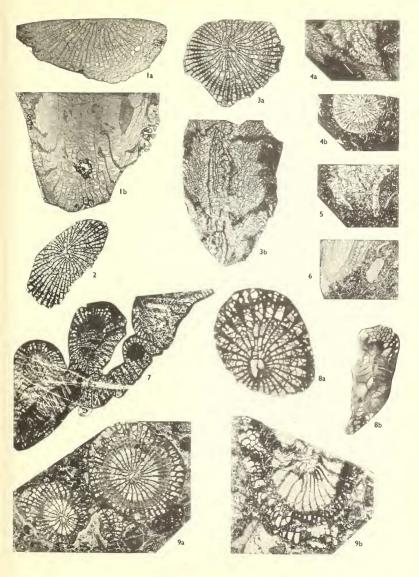
Plate 73, fig. 3

Material. SU 20102 (Pl. 73, fig. 3), loc. Cr-106; SU 17117, loc. Gn-10.

Description. The two known specimens are small, trochoid corallites; the epitheca is without septal grooves, but bears strong growth wrinkles. The calix is unknown.

#### EXPLANATION OF PLATE 72

- Figs. 1–3. *Mansayphyllum bellense* sp. nov. 1 *a, b,* Holotype SU 11295; transverse (*a*) and longitudinal (*b*) sections; celluloid 'peels', × 2. 2, Topotype SU 12110; transverse section, showing elongate cardinal and counter septa, × 2. 3 *a, b,* Topotype SU 20099; transverse (*a*) and longitudinal (*b*) sections, × 2 (see also text-fig. 7e). All from loc. Be-10.
- Figs. 4–6. *Mansuyphyllum parvulum* sp. nov. 4*a*, *b*. Topotype SU 14223, loc. Ct–40; longitudinal section (*a*) showing lateral talons, and transverse (*b*) section, ×4 (see also text-fig. 7*a*). 5, SU 18151, loc. CAT/255; longitudinal section of fragmentary corallite, ×4 (see also text-fig. 3*b*). 6, Holotype SU 14224, loc. Ct–40; longitudinal section—celluloid 'peel'—×4 (see also text-fig. 3*a*).
- Fig. 7. Zelolasma gemmiforme (Etheridge fil.). SU 5278, loc. MM-I0, figured Hill (1942c, pl. 6, fig. 6); transverse and longitudinal sections of corallites growing on the surface of a large solitary rugose coral (not shown); ×4 (see also text-fig. 5). Photograph courtesy Prof. D. Hill.
- Figs. 8 a, b. Mansuyphyllum catombalense subsp. nov? SU 13268, loc. Cr–100; transverse (a) and longitudinal (b) sections of fragmentary corallite, ×4 (see also text-fig. 7f).
- Figs. 9 a, b. Mansuyphyllum sp. A. SU 20101, loc. Be–10; transverse (a) and longitudinal (b) sections, × 4 (see also text-fig. 7c).



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Dimensions in mm.

Specimen	Dc	Dt	Dt/Dc	n	$L_1$	$L_2$
SU 20102	6.0	2.0	0.33	36	$\frac{2}{3} R$	2 R
SU 17117	7.5	3.0	0.40	38	3 R	2 R

The septa are strongly fusiform, the major little longer than the minor, and extending axially about  $\frac{2}{3} - \frac{3}{4} R$ . The minor septa end at the margin of the tabularium. In one specimen the septal dilatation is so strong that it forms a stereozone encompassing all but the outer 0-8 mm. of the dissepimentarium. In both specimens, there are numerous yardarm and zigzag carinae in the outer part of the dissepimentarium. The trabeculae are almost parallel, slightly axially directed, the inclination from the vertical being only a little greater at the tabularium than at the periphery. The tabularium is  $\frac{1}{3} - \frac{3}{2} Dc$  across; in the one available longitudinal section it is composed of irregular, distant, complete, flat to domed tabulae. In the same section, there are about four series of small, highly globose dissepiments, moderately inclined towards the axis.

Comparison. Mansuyphyllum sp. B differs from M. parvulum in the different trabecular structure of its fewer septa, and in having a uniseriate tabularium.

Remarks. This species is doubtfully included in Mansuyphyllum, because it does not have the biseriate tabularium characteristic of the type species. The carinate septa suggest Tipheophyllum, but that genus also has a biseriate tabularium, divided at the ends of the major septa. Further material is required before the precise affinities of this species are known, and until then it is best left un-named.

## Mansuyphyllum sp. C

Plate 73, fig. 6

Material. SU 17117 (Pl. 73, fig. 6), 17118, loc. Gn-10.

**Description.** The external shape is unknown, both specimens being worn. The calix has a sharp rim, steep walls, and a wide flat floor. *Dc* is at least 3 cm.

Dimensions in mm.

The major septa equal about  $\frac{3}{4}R$ ; they are radial, and straight or slightly wavy. The minor septa, only about  $\frac{1}{3}R$ , terminate within the dissepimentarium. The septa are fusiform, moderately dilated, the major more than the minor; they are thin in the tabularium. The zone of maximum dilatation is about the middle of the dissepimentarium.

The trabeculae form disphylloid fans, with the zone of divergence in the middle of the dissepimentarium. Peripherally they are slightly outwardly directed, and towards the tabularium they are increasingly axially directed, so that at the margin of the tabularium they are inclined at 60° from the vertical.

The tabularium is wide—at least  $\frac{1}{2}$  Dc. It is biseriate. The wide axial series consists of complete and incomplete tabulae, forming flat-topped domes. The narrower periaxial series consists of numerous horizontal and slightly outwardly inclined globose to sagging tabellae. Many of the tabulae are quite thickly coated with fibrous sclerenchyme.

The dissepimentarium contains nine or ten series of dissepiments. The outermost two to four series are small, globose, and vary from slightly outwardly inclined at the periphery, to horizontal in the zone of maximum septal dilatation, where they are often coated by extensions of the septal tissue. Axially from here, the dissepiments are increasingly inwardly inclined and elongate, until at the margin of the tabularium they are nearly vertical.

Comparison. These specimens differ from the type species in their slightly greater size, in a wider tabularium, and in the more dilated septa. From M. bellense they differ in having a relatively wider tabularium. From other Australian species of the same size they differ in the form of the tabularium. Further material is required, but it may be possible that these specimens are closely related to M. bellense.

### Genus ZELOLASMA Pedder 1964

1964 Zelolasma Pedder, p. 364.

Type Species: Diphyphyllum gemmiformis Etheridge fil. 1902, pp. 253-5, pl. 37, fig. 1; pl. 39, figs. 1, 2; pl. 40, fig. 1.

Diagnosis. Phaceloid to subcerioid disphyllid with frequent multiple peripheral budding. Septa subequal, generally thin, smooth peripherally, but wavy, slightly carinate, and sometimes slightly dilated, axially. Trabeculae in half-fans. Narrow dissepimentarium of a few series of small globose plates. Tabularium dominantly uniseriate, of gently sagging tabulae.

Remarks. Of the other phaceloid disphyllids so far described, Disphyllun has a biseriate tabularium (in the type species—see Hill 1939a, p. 225), Cylindrophyllun has well-developed yardarm carinae, and Acinophyllun McLaren has unequal septa, peripherally carinate, and prominent connecting processes. The new genus Paradisphyllun, described below, has a considerably more complex structure. See also p. 535.

Zelolasma gemmiforme (Etheridge fil. 1902)

Plate 72, fig. 7; text-fig. 5

For complete synonymy, see Pedder 1964, p. 365.

#### EXPLANATION OF PLATE 73

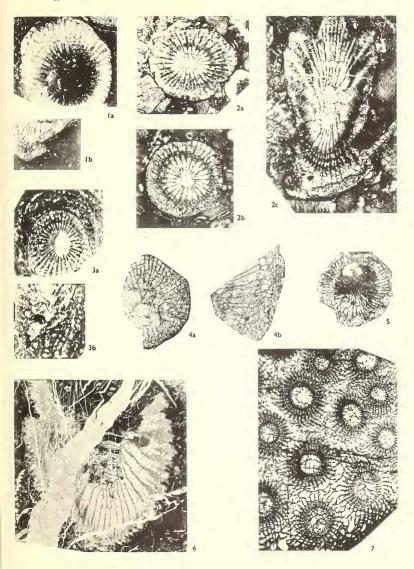
Figs. 1 a, b. Mansuyphyllum parvulum sp. nov. Holotype SU 14224, loc. Ct-40; (a) transverse section through calice (see also text-fig. 7b), (b) oblique longitudinal section; ×4.

Figs. 2a-c. Mansupphyllam catombaleuse sp. nov. Holotype SU 14155, loc. Ct–18; (a, b) transverse sections of two corallites, (c) longitudinal section; note septal discontinuity in b, c; ×4 (see also text-fig. 7d). 2a, b, photographs by Mr. A. G. Smith, University of Queensland.

Figs. 3 a, b. Mansuyphyllum? sp. B. SU 20102, loc. Cr–106; transverse (a) and longitudinal (b) sections of corallite surrounded by a stromatoporoid: ×4.

Figs. 4, 5. *Disphyllum* sp. cf. *gregorii* (Etheridge fil.). 4a, b, SU 16143, loc. E–16; transverse (a) and longitudinal (b) sections, × 2. 5, SU 16153, loc. E–21; transverse section through base of calix, × 2. Fig. 6. *Mansuphyllum* sp. C. SU 17117, loc. Gn–10; oblique longitudinal section, × 2.

Fig. 7. Phillipsastrea oculoides Hill. Holotype SU 5281, loc. MM-10; figured Hill (1942c, pl. 6, fig. 9); transverse section, ×2. Photograph courtesy Prof. D. Hill.



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Holotype, AM F 5171: Cavan Bluff Limestone, Taemas bridge, north bank of Murrumbidgee R., parish Warroo, near Yass, N.S.W. See also Pedder 1964, p. 365.

Material figured, SU 5278, loc. MM-10; figured Hill (1942c, pl. 6, fig. 6).

Diagnosis. As for the genus.

Remarks. Pedder has noted that the figures of maximum Dc and n given by both Etheridge Jr. and Hill are too low, and has given corrected values of Dc = 13.0 mm., and n = 50.

The specimen figured herein and by Hill (1942c) from the Garra Formation agrees very closely with the type material. Pedder, in his synonymy, queries inclusion of this specimen in the species, but I do not consider this doubt to be justified. As no further Garra material is available, no additions to existing descriptions are possible.

Known range. The species is so far known from the Couvinian? of the Murrumbidgee River area (Siegenian?, according to Pedder, p. 365), and from a locality (MM-10) in the Garra Formation probably towards the top, and most likely of early Couvinian or late Emsian age.



TEXT-FIG. 5. Portion of a small colony of Zelolasma gemmiforme (Etheridge fil.) adhering to the surface of another rugosan: traced from photograph (Pl. 72, fig. 7). SU 5278, figured Hill (1942c, pl. 6, fig. 6).  $\times 4$ .

## Genus DISPHYLLUM de Fromentel 1861

- 1861 Displyllum de Fromentel, p. 302 (fide Lang, Smith, and Thomas 1940, p. 53).
- 1893 Cannophyllum E. J. Chapman, p. 45 (obj. syn., Stumm 1949, p. 33).
- Disphyllum de Fromentel; Lang and Smith, p. 545 (partim). This paper contains a very 1935 full synonymy to 1935; however, the authors took a broad view of the genus, which has not been substantiated by recent workers.
- 1956 Disphyllum de Fromentel; Hill, p. F280, in Moore, (See for further synonymy, post-1935,)

Type species: Cvathophyllum caespitosum Goldfuss 1826, p. 60 (partim) = Disphyllum goldfussi (Geinitz 1846); subsequent designation Lang and Smith 1934, p. 80.

Diagnosis, Fasciculate Disphyllidae with smooth septa, whose maximum dilatation is peripheral; tabularium biseriate, the periaxial tabellae axially inclined; several series of globose dissepiments; trabeculae parallel or in half-fans.

Discussion. As shown by Lang and Smith (1934, 1935), and also by Smith (1945, p. 21), the holotype of D. goldfussi has smooth septa which are moderately dilated in the dissepimentarium (particularly at the periphery) and thin in the tabularium. The tabularium is biseriate, and the dissepimentarium consists of several series of dissepiments. Other fasciculate disphyllids are Cylindrophyllum Simpson 1900, Acinophyllum McLaren 1959, Zelolasma Pedder 1964, and Paradisphyllum sp. nov. The first is characterized by strongly developed yardarm carinae in both dissepimentarium and tabularium, and by a fairly narrow dissepimentarium. Acinophyllum was erected to include those American disphylloid species previously placed in Synaptophyllum Simpson 1900, which McLaren has shown to be a stauriid. The type species is characterized by a narrow dissepimentarium,

a uniscriate tabularium, septa which are weakly dilated peripherally and zigzag carinate in the dissepimentarium, and numerous connecting processes. *Zelolasma* differs from *Acinophyllum* principally in lacking the connecting processes, and in having subequal septa which are only carinate (and sometimes slightly dilated) axially. All three genera have trabeculae either subparallel or arranged in half-fans. *Paradisphyllum* has a more complex structure, with strong disphylloid trabecular fans, a wide dissepimentarium, and a biseriate tabularium.

The simplicity of the tabularium in *Acinophyllum* is one of the diagnostic features stressed by McLaren. However, the taxonomic value of this feature is debatable. Thus *Sudetia* Różkowska 1960, has as type a species in which both uniseriate and biseriate tabularia occur. Those specimens with a uniseriate tabularium resemble very strongly *Acinophyllum*. This raises the question of the validity of both genera. *Sudetia* was erected for a 'descendant form' of *Peneckiella minor kunthi* (vide Różkowska 1960, p. 33), in which the horseshoe dissepiments have become obsolete. However, the dissepimental types figured for *Sudetia lateseptata*, the type, are not even 'peneckielloid' (see p. 556). Moreover, I find it difficult to see how *S. lateseptata* can be a descendant of *Peneckiella minor kunthi* (Dames), as the former species is known only from the one locality, where it is intergrown with its supposed predecessor. It is likely that *Sudetia* Różkowska 1960, is a junior synonym of *Acinophyllum* McLaren 1959.

## Disphyllum gregorii (Etheridge fil. 1892)

1892 Campophyllum gregorii Etheridge fil. in Jack and Etheridge Jr., p. 60, pl. 3, figs. 15–18, Locality—Reid Gap, N. Qld.; Givetian.

1895a Campophyllum gregorii Etheridge fil. p. 522, pl. 40, fig. 2. Locality—the same.

1942a Disphyllum gregorii (Etheridge); Hill, p. 247, pl. 8, figs. 1–4. Locality—the same, also Fanning R. and Burdekin Downs areas; Givetian.

non 1912 Campophyllum gregorii Etheridge; Chapman, p. 219, pl. 34, figs. 3–5, which is Breviphyllum recessum (Hill 1940).

Lectotype. By subsequent designation Hill 1942a, p. 247. GSQ F 1655; figured Etheridge Jr., pl. 3, fig. 15, in Jack and Etheridge Jr. 1892.

Type locality. Regan's Limestone Quarry, probably portion 397v, parish Magenta; Reid Gap, near Townsville, N. Queensland. Reid River Limestone, Givetian (Hill 1942a).

Diagnosis. 'Disphyllum with ceratoid to cylindrical corallites with about 30 septa of each order; typically the major septa reach about half way to the axis, while the minor septa are less than half as long; there is typically one or two series of small, very globose dissepiments, and the septa are dilated so that they extend laterally over the upper surfaces of the dissepiments; typically the tabulae are complete and horizontal, supplemented at the margins by smaller plates; variability is great; the number of series of dissepiments may increase, the septa may become long, and sometimes curved about a small axial space, when the tabulae become incomplete on concave floors; the dilatation of the septa varies in amount and position.' (Hill 1942a, p. 248.)

Remarks. Points of difference of *D. gregorii* from *Breviplyllum recessum* not brought out in the descriptions of Hill (1940, 1942a) are: firstly, in *B. recessum* the septa are thin, relatively short, and in transverse section exhibit discontinuities within the tabularium.

In *D. gregorii* the septa are usually dilated at some point in their length, and are never discontinuous. The trabeculae in *D. gregorii* are thick monacanths, subparallel, and directed axially at a high angle from the vertical; trabeculae are not visible in the holotype of *B. recessum*. Finally, the epitheca of *B. recessum* is marked by deep, narrow septa grooves, separated by wide flat interseptal 'ridges'. The septal grooves in *D. gregorii*, when developed, are very shallow and wide, essentially the intersection of two neighbouring slightly rounded to flat interseptal ridges.

Disphyllum sp. cf. gregorii (Etheridge fil. 1892)

Plate 73, figs. 4, 5

Material. Several fragments from locs. Cr-12, E-16, and E-21.

Figured specimens. SU 16143 (loc. E-16), 16153 (loc. E-21).

Description. The available fragments vary somewhat in structure, some sections being very like some figured sections of B. recessum (Hill 1940b, e.g. pl. 9, fig. 7). However, the Garra specimens all have about sixty septa, with Dc = 13-16 mm., contrasting with n = 44 and Dc = 10 mm. for normal B. recessum. They also have the type of septal groove found in D. gregorii, and continuous septa.

Dimensions in mm.

Specimen	Locality	Dc	Dt	Dt/Dc	n	$L_1$	$L_2$
SU 16143	E-16	15	9.5	0.63	c. 70	$c. \frac{1}{2} R$	$c. \frac{1}{3} R$
SU 16145	,,	> 11.5	9.5	< 0.83	64	$\frac{1}{2}R$	$\frac{1}{4}R$
SU 16153	E-21	c. 14	8.0	c. 0.57	66	c. R	$c. \frac{1}{3} R$

The specimens agree most closely with Hill's description of specimens from the Reid Gap area, in that all have about five or six series of dissepiments, and highly variable septal length and dilatation. Generally the septa dilate at the margin of the tabularium, where the dilatation may spread over the dissepiments, and then they either remain at a constant moderate dilatation throughout the dissepimentarium, or show successive moderate wedge-wise dilatations over the surfaces of successive series of dissepiments. However, this may vary even in the one transverse section, with the septa on one side remaining attenuate throughout. Similarly the tabularium is variable; in some cases the tabulae are complete, flat with down-turned edges, supplemented by periaxial inclined tabellae; in others, the tabulae are incomplete and sagging, and the periaxial tabellae are both more numerous and less regular in size.

Unfortunately none of the sections is sufficiently well preserved to show clearly the trabecular structure. There is a suggestion that the trabeculae are thin, and axially directed at a large angle from the vertical (as in *D. gregorii*), but I have not seen the thick monacanths so characteristic of the Oueensland species.

# Genus paradisphyllum gen. nov.

Type species. Paradisphyllum harundinetum sp. nov.

*Diagnosis.* Fasciculate disphyllids with septal trabeculae arranged in disphylloid fans. Septa fusiform, carinate outside the zone of greatest dilatation; the counter septum

may be elongate. Minor septa, and sometimes major septa, discontinuous near periphery. Tabularium as in *Disphyllum*.

Remarks. Paradisphyllum differs from other fasciculate disphyllids essentially in the arrangement of the trabeculae in marked disphylloid fans (see p. 523), and so in having a calix with a strongly reflexed rim. The type species is further distinguished by having discontinuous septa.

I would tentatively include in *Paradisphyllum* the Victorian species *Disphyllum cognatum* Philip 1962 (p. 177, pl. 24, figs. 5, 10, text-fig. 4b), from the Gedinnian Cooper's Creek Formation. This species has a similar trabecular arrangement to that of *P. harundinetum*; the only essential differences are that apparently the major septa are of uniform length, and that the septa are continuous. I consider that the trabecular structure is of far greater significance than the septal discontinuities.

Another possible species is *D.* [Synaptophyllum] densum Smith 1945 (p. 22, pl. 12, figs. 3 a-c). As described and figured by Smith, this species has all the diagnostic features of Paradisphyllum. However, McLaren (1959, p. 30) has noted that horseshoe dissepiments are present in one longitudinal section of Smith's type material. All the other longitudinal sections show trabecular fans, and so McLaren has tentatively assigned the species to Phacellophyllum. Further study is needed on this matter.

Range. Paradisphyllum is definitely known from the Emsian or early Couvinian of the Garra Formation, and is probably also represented in the Gedinnian of Victoria. It may also be present in the Frasnian of Canada.

Paradisphyllum harundinetum gen. et sp. nov.

Plate 74, figs. 1, 3; text-figs. 6, 7g, h

Holotype. SU 13236 (Pl. 74, fig. 1), loc. Cr-100. Paratype SU 20100 (Pl. 74, fig. 3).

Derivation of name. Latin harundinetum, a thicket of reeds; refers to the appearance of the trabeculae in longitudinal section.

Diagnosis. Dendroid to subcerioid Paradisphyllum about 7 mm. in diameter, with both orders of septa frequently discontinuous peripherally; with very irregular dissepiments, and crowded tabulae.

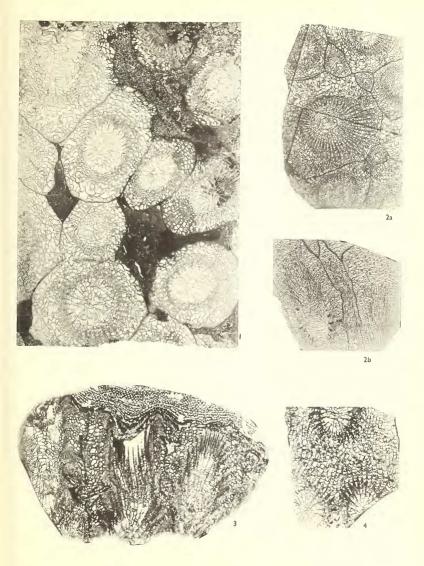
Description. The corallum is small, generally dendroid, and usually in the form of a low dome. In crowded, subcerioid parts, individual corallites are bounded by slightly curved to irregular walls; otherwise they may be separated by up to 1 cm., when they are ceratoid to cylindrical. The calix has a wide reflexed rim surrounding a shallow cup-shaped axial depression. Budding is lateral. Dc of adults = 5–11 mm., those near the mode being 6–7·5 mm.

#### EXPLANATION OF PLATE 74

Figs. 1, 3. Paradisphyllum harundinetum gen. et sp. nov. 1, Holotype SU 13236, loc. Cr–100; ×4 (see also text-fig. 7h); specimen collected by Dr. J. R. Conolly. 3, Paratype SU 20100, loc. Cr–100; longitudinal section, ×4 (see also text-fig. 7g).

Figs. 2 a, b. Hexagonaria approximans cribellum subsp. nov. Holotype SU 13259, loc. Cr–100; transverse (a) and longitudinal (b) sections, ×2; specimen collected by Dr. J. R. Conolly.

Fig. 4. Billingsastraea aperta (Hill). SU 13261, loc. Cr-100; transverse section of corallum with relatively strong septal dilatation, ×2.



STRUSZ, Australian Devonian Rugosa



Dimensions in mm.	Specimen	Dc	Dt	Dt/Dc	n
	(max.	11.2	4.2	0.78	44
	SU 13236 mean	6.6	2.9	0.46	36
	min.	1.2	0.9	0.33	6
	No. of readings	33	33	33	33
	(max.	8.0	3.6	0.51	34
	SU 20100 mean	6.3	2.8	0.45	
	min.	4.4	1.9	0.39	32
	No. of readings	6	6	6	2

The thin epitheca shows strong transverse growth irregularities, but no septal grooves; it is lined by a thin (0.2 mm.) fibrous stereozone, from which project the septa. For adults, n is generally 38–42. The major septa are long, straight in the wide dissepimentarium, and straight or slightly curved in the tabularium. They are unequally withdrawn from the axis, leaving a space 1–1.5 mm. across, into which the counter septum, and sometimes the cardinal septum, projects. The septa often show a moderate pinnate arrangement about the counter-cardinal plane, in which case the counter-lateral septa may be slightly withdrawn; however, the septa may be completely radial.  $L_2$  is about  $\frac{1}{2}$  to  $\frac{2}{3}$  R; the minor septa end just inside the tabularium.

The septa are fusiform, and may be so strongly dilated as to form a stereozone up to 1 mm. wide near the inner margin of the dissepimentarium. However, the degree of dilatation is highly variable, even from one side of a corallite to the other, and in some juveniles it may be entirely absent. Towards the periphery the septa generally become attenuate, and bear irregular zigzag carinae. In this zone the minor septa are generally more or less discontinuous; less commonly the major septa also break up into discontinuous fragments.

The monacanthine trabeculae are arranged in broad disphylloid fans, closely resembling those which characterize the family Phacellophyllidae. The zone of divergence of the trabeculae corresponds exactly with the zone of maximum septal dilatation, at about the mid-radius, and about two-thirds of the way from the periphery to the tabularium.

The biseriate tabularium is about  $\frac{2}{5}-\frac{1}{2}$  Dc across, and consists of numerous closely crowded tabellae. The axial series is of globose plates, arranged in broad domes, and interfingering marginally with the periaxial tabellae, which are flat or gently sagging.

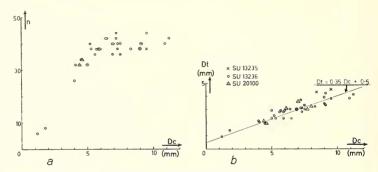
The dissepiments are small, globose, in five to eight series. Their inclination varies from vertical at the inner margin of the dissepimentarium, through horizontal in the zone of maximum septal dilatation, to moderately outwardly inclined outside this zone. In this outer zone the dissepiments may become lonsdaleoid.

Variation. As only one of the colonies so far found is relatively large and the total material is limited there are not enough data for a detailed study of intra-specific variation. No strong correlation between n and Dc could be found (text-fig. 6a), but a plot of Dt against Dc (text-fig. 6b) was clear enough to give a growth equation of Dt = 0.35 Dc + 0.5.

Comparison. P. harundinetum is apparently one of a group of closely similar disphyllid corals occurring in the Garra Formation, and is probably derived from one of these by acquisition of a colonial habit. The group is discussed below.

Known localities. This species is only known from the biostrome at loc. Cr-100.

Discussion of Phylogeny. During examination of sections of a large number of Garra disphyllids, it became apparent that many of them had several fairly distinctive features in common, suggesting that they may be in fact closely related. To check this, their salient features were compared in a chart (p. 531), and plots of available data for n/Dc and Dt/Dc were made. These show that the various species within this group of Garra disphyllids are indeed probably closely related, and a study of their stratigraphic distribution, in so far as it is known, further suggests a phylogenetic plexus, of which the progenitor is probably the small solitary coral M. parvulum (known from beds closer to the base of the formation than those containing the other species).



TEXT-FIG. 6. Plots of (a) n against Dc and (b) Dt against Dc, for three specimens of Paradisphyllum harundinetum gen, et sp. nov.

The features common to the species of this postulated plexus, and which distinguish them from other Garra disphyllids, are:

- (1) Strongly fusiform septa, peripherally weakly to strongly carinate.
- (2) Trabeculae arranged in half-fans or full disphylloid fans.
- (3) Long major septa, frequently pinnate about the counter-cardinal plane.
- (4) Counter septum elongate, generally reaching the axis, and in some extending completely across the axial space.

The differences between the various species are summarized in the table, p. 541. Note that for M. catombalense and P. harundinetum, the data for Dt/Dc, while rather limited, are sufficiently closely correlated to allow the determination of approximate growth equations (see also text-figs. 4, 6).

The inferred relationships of the species are shown in text-fig. 7. The most nearly certain is the lineage *M. parvulum—M.* sp. A—*M. catombalense*, while the least certain is *M. bellense*. The latter shares with the others most of the features distinctive of the group, but is considerably larger. As intermediate specimens have not been found, the relationship of *M. bellense* to the remaining species is as yet uncertain.

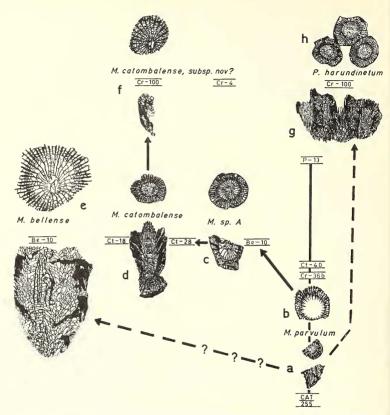
Paradisphyllum	harundinetum	dendroid - subcerioid	1:2 - 11:2 mm	6 – 7·5 mm	0.35 Dc + 0.5	1:0 — 1:5 mm		977 - 9	c. 40	0.8 - 0.9 R	0-5-0-7R	may be peripherally discontinuous		numerous	frequently, moderately	variable length	may be slightly withdrawn	sometimes elongate	5 - 8	1
	catombalense subsp. nov?	ceratoid?	15 + mm	ć	ċ	1.7 x 1.2 mm		c.	5 7 5	0.8 R	>0.3R	continuous?	- discontinuous	common?	strongly	1	withdrawn	elongate	6 <	c. 0-3 R
4	catombalense	ceratoid	1.6 - 8.7 mm	7 – 8 mm	0.5 Dc + 0.4	c. 1 mm		28-48	c. 42	9 R	5.R	1		common	lys ———— syl		withdrawn	1	1 – 5	
Mansuyphyllum	sp. A	c.	5.4 - 9.6 mm	9 mm	٠	1.0 x 0.6 mm		36-50	c 50 ?	C. 0.9 R	C. 0.5R	snon		fairly common	elways	elongate	slightly v	-equal to metasepta-	5-7	2 R
Ma	parvulum	turbinate-trochoid	5·2 - 10·1 mm	9 – 10 mm	ć	c. 2 mm		32+-52	c. 50	c. 0.7 R	0-3 - 0-5 R	continuous	- continuous	- infrequent	sometimes, slightly		metasepta	b <sub>3</sub> —————	3-4	C. 0.2 R
	bellense	trochoid?	20+ - 30·5+ mm	25 – 30 mm	5	c. 3mm		c. 50 - c. 76	≥ 60	) 0.9 R	>0.5R	•		infre	frequently	<b>\</b>	cqual to	elongate	9 - 14	c. 0.5 R
GENUS	Characters	Corallum:	known range:	~	Growth curve, Dt =	Diameter, axial space:	SEPTA:	known range:	nor )	Lı	L <sub>2</sub>	continuity ( major :	minor:	carinae in diss'arium :	Septal pattern: pinnate?	×	KL	ပ	Series of dissepiments:	Width of diss'arium:

Table comparing importance features of Paradisphyllum harundinetum gen. et sp. nov., and those species of Mansuphyllum which are considered to be phylogenetically related.



GENUS		Ма	insuyphyllu	m		Paradisphyllum
species Characters	bellense	parvulum	sp. A	catambalense	catambalense subsp. nav?	harundinetum
Corallum:	trochoid?	turbinate-trochoid	?	ceratoid	ceratoid ?	dendroid — subcerioid
(known range:	20+ - 30 5+ mm	5-2 - 10-1 mm	5-4 - 9-6 mm	1-6 - 8-7 mm	15 + mm	1-2 - 11-2 mm
Dc \ No freadings: normal adults:	25 ~ 30 mm	9 – 10 mm	9 mm	7 – 8 mm	3	6 - 7·5 mm
Growth curve, Dt =	?	?	?	0-5 Dc + 0-4	?	0.35 Dc + 0.5
Diameter, axial space :	c. 3 mm	c. 2 mm	1-0 x 0-6 mm	c. 1 mm	1-7 x 1-2 mm	1·0 — 1·5 mm
SEPTA:						
(known range:	c.50 - c.76	32+ 52	36-50	28-48	? /	6-44
n { N° of readings: normal adults:	≥ 60	c. 50	c 50 ?	c. 42	54 ?	c. 40
Lı	> 0·9 R	c. 0·7 R	<b>←</b>	9 R	0-8 R	0-8 - 0-9 R
Lz	> 0·5 R	0·3 - 0·5 R	<b>←</b> c. 0	5R	> 0·3 R	0·5 - 0·7 R
continuity { major:	<	contir	nuous		continuous?	may be peripherally discontinuous
minor:	<del>-</del>	— continuous —		<b>←</b>	- discontinuous -	-
carinae in diss'arium :	infr infr	equent ———	fairly common	common	common?	numerous
Septal pattern: pinnate?	frequently	sometimes, slightly	← alw	ays —	strongly	frequently, moderately
К	<del></del>		elongate -		$\longrightarrow$	variable length
KL	equal to	metasepta		withdrawn ———	withdrawn	may be slightly withdrawn
С	elongate	←	qual to metasepta		elongate	sometimes elongate
Series of dissepiments:	9 — 14	3-4	4-5	1 ~ 5	≥ 9	5 -8
Width of diss'arium:	c. 0.5 R	<b>←</b> c. 0	2 R	<b>—</b>	c. 0-3 R	$\rightarrow$

Table comparing importance features of Paradisphyllum harundinetum gen. et sp. nov., and those species of Mansuyphyllum which are considered to be phylogenetically related.



TEXT-FIG. 7. Inferred phylogenetic relationships between species of *Mansuyphyllum*, and *Paradisphyllum harundinetum*; all ×1·5, traced from photographs (see Pl. 72–74). Localities from which the various species are known are shown in their probable relative stratigraphic positions; where known with reasonable accuracy, these are in heavy lettering. *a*, Transverse and longitudinal sections, SU 14223 (loc. Ct–40). *b*, Transverse section through calix, holotype SU 14224 (loc. Ct–40). *c*, Transverse and longitudinal sections, SU 20101. *d*, Transverse and longitudinal sections, holotype SU 14155.

q. Transverse and longitudinal sections, paratype SU 20099. *f*, Transverse and longitudinal sections, SU 13268. *g*, Longitudinal section, paratype SU 20100. *h*, Transverse section, holotype SU 13236.

## Genus HEXAGONARIA Gürich 1896

1896 Hexagonaria Gürich, p. 171 (fide Lang, Smith, and Thomas 1940, p. 69).

1949 Hexagonaria Gürich, Stumm, p. 33. See for list of synonyms.

1954 *Hexagonaria*, Moenke, p. 452. See for a full discussion of the genus (taxonomy and morphology).

Type species. By subsequent designation Lang, Smith, and Thomas 1940, p. 69, Cyathophyllum hexagonum Goldfuss 1826, p. 61, pl. 19, figs. 5 e, f, pl. 20, figs. 1 a, b; non pl. 19, figs. 5a-d.

Diagnosis. 'Cerioid corals with individual corallites separated by polygonal walls. Calices usually with an axial pit and a peripheral platform. Septa radially arranged, of two orders, major extend into tabularium while minor are confined to dissepimentarium. They are lightly or heavily carinate, rarely dilated. No modification of protosepta is visible. Dissepimentarium is wide and composed of many rows of horizontal or inclined dissepiments. Tabularium is relatively narrow and composed of closely set, complete or incomplete tabulae, that are horizontally disposed.' (Stumm 1949, p. 33.)

Discussion. A list of synonyms may be found in Stumm (1949). It should be noted also that in many cases Soshkina has included in her genus Megaphyllum species which are Hexagonaria, as well as some, including the type, which are considered by Stumm (1949) and others to be *Disphyllum*. In her discussion of *Megaphyllum* (1954, p. 37), Soshkina referred critically to Stumm's illustration of H. hexagona (1948, pl. 6, figs. 1, 2), stating that fig. 1 is of the holotype, and fig. 2 of a different species. Yet according to Stumm, both are sections of the same specimen, a hypotype. Still referring to this, Soshkina also stated: '... [Stumm] cannot distinguish the species of the genus *Phillipsastraea* from the massive colonies belonging to the group of species "Cyathophyllum hexagonum Goldf.", in other words belonging to genus Megaphyllum Soshk.....' This, with other statements on the same page, apparently indicates that Soshkina considered the type species of Hexagonaria to be a species of her genus Megaphyllum. At the same time, she placed Prismatophyllum Simpson 1900, in synonymy with Megaphyllum. In both cases, there is clear contravention of the rules of nomenclatural priority (Stoll et al. 1961: Art. 23). This apparent confusion of type species and of priority has unfortunately caused considerable divergence of usage in the work of authors from Europe, America, and Australia on the one hand, and from Russia on the other.

Megaphyllum bulvankerae Soshkina 1954 (p. 38) and M. columellare Soshkina 1954 (p. 40) are species of Hexagonaria.

# Hexagonaria approximans (Chapman 1914)

1914 *Cyathophyllum approximans* Chapman, p. 304, pl. 47, figs. 5, 6. East Gippsland, Victoria: Early Devonian.

1939a Prismatophyllum approximans (Chapman); Hill, p. 234.

1954b Hexagonaria approximans (Chapman); Hill, p. 107, pl. 6, figs. 3 a, b.

1954b Hexagonaria aff. approximans (Chapman); Hill, p. 108, pl. 6, figs. 4a, b. Waratah Bay, Victoria: Bell Point Limestone, 'possibly Couvinian'.

1962 Hexagonaria approximans (Chapman); Philip, p. 177, pl. 24, figs. 4, 8, 9. Tyers R., Gippsland, Victoria: Cooper's Creek Formation, early Gedinnian.

*Holotype*, NM 1247: specimen figured Chapman 1914, pl. 47, figs. 5, 6. Quoted and figured as holotype by Hill 1954*b*, p. 107, pl. 6, figs. 3 *a*, *b*. Type locality given by Chapman as 'Cooper's Creek, behind

Chinaman's Garden'; probably from the early Gedinnian Cooper's Creek Formation of Philip 1962, p. 127. Chapman also listed specimen no. 746, but this is not quoted by either Hill or Philip.

*Diagnosis.* Large *Hexagonaria* with thirty-two to forty-two long, slightly fusiform septa, with carinae well developed near periphery; trabeculae arranged in half-fans or in broad disphylloid fans; tabularium narrow, biseriate.

Remarks. This species has been well described by Philip (1962) who, from the type material and a large collection from the Tyers River area, was able also to assess variation, which he found to be considerable. One point to note is that according to Philip the trabeculae are directed inwards at all times, whereas according to Hill (1945b, p. 107) '... there may be an area of divergence ... near the inner margin of the dissepimentarium'. This is not clear in her figures of the holotype, but is quite definite in her H. aff. approximans (pl. VI, fig. 4b), which Philip placed in synonymy with H. approximans.

Known range. The holotype comes from Cooper's Creek, probably from the same horizon as the Cooper's Creek Formation of Philip (1962), some miles to the south. Philip considered this horizon to be probably Gedinnian in age. The species is also known from the Bell Point Limestone of Waratah Bay, Victoria; Hill (1954b) considered this horizon to be '. . . possibly Couvinian'. Philip (1960b) placed it between the Cooper's Creek–Loyola faunas and the Buchan fauna, probably Siegenian.

Hexagonaria approximans cribellum subsp. nov.

Plate 74, figs. 2a, b; Plate 75, figs. 1a, b; text-figs. 8, 9

Holotype, SU 13259 (Pl. 74, figs. 2a, b), loc. Cr-100. Other material figured: SU 13260 (loc. Cr-100).

Derivation of name. Latin cribellum, a small sieve; in reference to the complex carinae.

Diagnosis. H. approximans with numerous strongly fusiform septa, and tabulae with upturned margins.

Description. All known coralla are small, and apparently in the shape of low domes. The calix has a narrow rim, either flat or slightly everted, and rather steep sides surrounding a relatively shallow axial pit whose floor is gently domed.

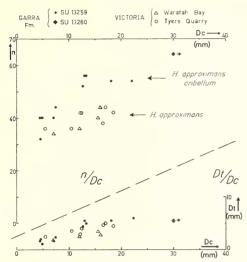
Dimensions in mm. (representative corallites).

Specimen	Dc	Dt	Dt/Dc	n	$L_1$	$L_2$
SU 13259	4.9	1.2	0.24	40	0.8 R	0·5-0·7 R
	12.7	4.4	0.35	52	0·7 R	0.6 R
	13.3	5.0	0.38	56	0.8 R	0.5 R
	22.1	6.0	0.27	54	0.8 R	0·7 R
SU 13260	> 30	5.5	< 0.18	64	c. 0.9 R	c. 0.8 R

In adult corallites, Dc is about 2 cm. Each corallite is bounded by a very thin epitheca, lined by a fibrous stereozone 0-2-0-5 mm. thick. For adults, n = 54-64. The major septa are long, leaving an axial space of 3-4 mm.; the minor septa are little shorter, and end at the margin of the tabularium. Attenuate in the tabularium, the septa are strongly fusiform in the dissepimentarium, with the zone of maximum dilatation being  $\frac{1}{3} - \frac{1}{2}R$  in from the periphery. Peripherally the septa are generally thin, but bear prominent,

flanged zigzag carinae, and occasionally break up into naotic segments consisting of these complex carinae without the intervening lamellar portions of the septa.

The thin trabeculae are arranged in strongly asymmetrical disphylloid fans, the zone of divergence approximately corresponding to the zone of maximum septal dilatation. At the periphery the trabeculae are vertical, or more generally are inclined outwards



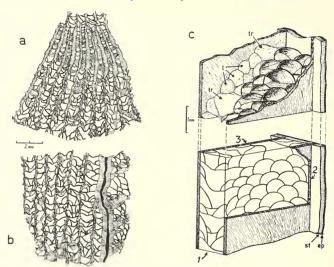
TEXT-FIG. 8. Plots of *n* (above) and *Dt/Dc* (below) against *Dc* for *Hexagonaria approximans* (Chapman) and *H. approximans* cribellum subsp. nov. Data for *H. approximans* s.s. obtained from published figures: Hill (1954b—Waratah Bay) and Philip (1962—Tyers Quarry).

at a small angle from the vertical. Inward from the zone of divergence they are increasingly curved, and at the margin of the tabularium they are generally inclined at a very high angle from the vertical, and may be horizontal. Within the tabularium their inclination becomes increasingly steep axially.

A plot of Dt against Dc shows a fairly strong correlation (text-fig. 8); for the holotype, the corresponding growth equation is approximately:  $Dt = 0.33 \, Dc$ . The tabular floors are flat or gently domed, with sharply upturned margins. The tabulae are crowded, complete or more usually incomplete, and slightly sagging to slightly domed. Those which abut against the dissepimentarium are moderately to sharply upturned marginally. Rarely, the tabulae are marginally supplemented by slightly globose tabellae, inclined towards the axis.

The wide dissepimentarium consists of up to eighteen series of small, highly globose

dissepiments, which are horizontal or outwardly inclined peripherally, horizontal until about the fourth series, then steeply and evenly inclined towards the tabularium until the last two to four series, which are vertical and elongate. Towards the periphery, the dissepiments in each interseptal loculus are frequently imperfectly arranged in three series: one series of transverse, cylindroidal plates, and two lateral series of convex,



TEXT-FIG. 9. Dissepimental structure, Hexagonaria approximans cribellum subsp. nov. a, Transverse section; b, tangential longitudinal section; SU 13260 (loc. Cr-100), ×5 (cf. Pl. 75, figs. 1a, b). c, Schematic representation, ×10; 1—tangential longitudinal section; 2—radial longitudinal section (part of septum removed to show dissepiments); 3—transverse section. ep—epitheca; st—peripheral stereozone: tr—transverse (cylindroidal) dissepiments; l—lateral dissepiments.

incomplete plates, resting partly on the sides of the septa, and partly on the cylindroidal plates or on each other (text-fig. 9).

Comparison. This subspecies differs from the original species principally in having considerably more septa—average about sixty as against about thirty-eight. This also shows up in plots of n against Dc for the two forms (text-fig. 8). In addition, the septa are in general more strongly dilated, and the trabeculae are arranged in more strongly developed fans. There seem to be more series of dissepiments, and the tabular floors tend to be sagging rather than domed. In other respects, including the high degree of variability (particularly in size), the new subspecies is quite close to H. approximans s.s.

Remarks. In view of the definite differences from the Victorian species, and in the interests

of stratigraphic precision, I feel it is desirable to separate the Garra form at the subspecies level. *H. approximans cribellum* is, however, quite probably a descendant of the Victorian species.

Known localities. Loc. Cr-100.

### Genus BILLINGSASTRAEA Grabau 1917

1917 Billingsastraea Grabau, p. 957 (fide Lang, Smith, and Thomas 1940, p. 27).

1958 Billingsastraea Grabau; Schouppé, p. 253. Contains an exhaustive synonymy.

Type species, Phillipsastrea verneuili Milne-Edwards and Haime 1851, p. 447, pl. 10, fig. 5 (fide Lang.,

Smith, and Thomas 1940, p. 27).

*Diagnosis*. Massive Disphyllidae with walls between corallites absent, or represented by fibrous sclerenchyme, but no epitheca. Septa may be confluent, abutting, or peripherally discontinuous.

Discussion. In an extensive study of the 'Phillipsastrea' group of Rugosa, Schouppé (1958) has shown that Phillipsastrea sensu stricto possesses a zone of horseshoe dissepiments, and so is a senior synonym of Pachyphyllum Milne-Edwards and Haime. Schouppé placed the species without horseshoe dissepiments in Billingsastraea. Until certain nomenclatural problems raised by this revision are resolved by the International Commission (see p. 524), I have accepted this re-assignment.

The following Australian species lack series of horseshoe dissepiments, and should, following Schouppé's revision, be placed in *Billingsastraea: Phillipsastraea aperta* Hill 1942b; *P. callosa* Hill 1942b; *P. carinata* Hill 1942; *P. delicatula* Hill 1936; *P. linearis* Hill 1942b (*P. walli* Etheridge of Chapman 1914, non Etheridge Jr. 1892); *P. maculosa* Hill 1942b; *P. speciosa* Chapman 1914.

P. currani Etheridge fil. 1892, poses a problem which can only be solved by further study. Some specimens from the type locality (Limekilns, north of Bathurst, N.S.W.) lack horseshoes, while others have perfectly developed series of horseshoes. It is possible that two species are present. P. oculoides Hill 1942c, possesses definite all horseshoe dissepiments, and so remains in Phillipsastrea d'Orbigny 1849, sensu Schouppé 1958. Phillipsastrea sp. Hill 1954a, p. 14, pl. 3, fig. 2, is probably a Billingsastraea, but no longitudinal section is available.

## Billingsastraea aperta (Hill 1942)

Plate 74, fig. 4; Plate 75, figs. 2, 3

1942b Phillipsastraea aperta Hill, p. 154 (non? pl. 2, figs. 7a, b). 1942c Phillipsastraea aperta Hill; Hill, p. 183, pl. 6, figs. 7a, b.

*Holotype*: SU 7289 (Pl. 75, figs. 3 *a*, *b*), loc. Cr–113. Other material figured: SU 13261, 20104, both loc. Cr–100.

*Diagnosis.* Astraeoid *Billingsastraea* with widely spaced and only slightly dilated septa, with numerous small globose dissepiments, and with elongate tabellae arranged on slightly domed tabular floors. (After Hill 1942b, p. 154.)

Description. The description given by Hill (1942b) is very brief, and so the species is redescribed below.

The corallum is partly astraeoid, partly thamnastraeoid. The calicular pits are rather deep, with steep walls, gently domed floors, and rounded everted rims. The pits are about 6 mm. in diameter, while *Ts* (see p. 522) is about 13 mm.

Dimensions in mm.

	Dt	n	n/Dt	Ts
Mean	5.2	38*	7.3	13.7
Max.	6.0	46	7.9	17.9
Min.	3.8	30	5.3	10.1
No. of readings	9	8	8	24

<sup>\*</sup> Mean n to the nearest even number. Data from 2 coralla, loc, Cr-100.

The major septa are long, leaving an axial space 1–2 mm. across, while the minor septa end just inside the tabularium. The axial space is elongate in the counter-cardinal plane; the cardinal septum projects a short distance into the space, but the counter septum extends right across it, its end either uniting with the cardinal septum, or turned abruptly aside. The remaining septa show a slight pinnate arrangement. The septa are fusiform; in a zone 2·5–3·5 mm. wide at the inner margin of the dissepimentarium they are usually as wide as the interseptal loculi. Away from this zone the dilatation decreases rapidly, the septa being attenuate peripherally and axially.

The slender trabeculae are arranged in well-developed asymmetrical disphylloid fans, whose zone of divergence corresponds exactly with the zone of maximum septal dilatation.

Dt = 3-5 mm.; the tabularia are composed of numerous flat or gently domed, complete and incomplete tabulae, arranged biserially. In the broad axial zone the tabulae are supplemented by moderately convex tabellae.

The dissepimentarium is composed of numerous small globose dissepiments, horizontal in the zone of maximum septal dilatation, steeply axially inclined inwards from this zone, and moderately peripherally inclined outside the zone. Midway between tabularia the dissepiments are again horizontal.

Comparison. B. aperta very closely resembles Pseudoacervularia roemeri (Verneuil and Haime 1850) of Różkowska (1953), from the Frasnian of the Holy Cross Mts., Poland. This resemblance is most noticeable in the arrangement of the dissepiments, the trabecular fans, and the degree of variation of septal dilatation.

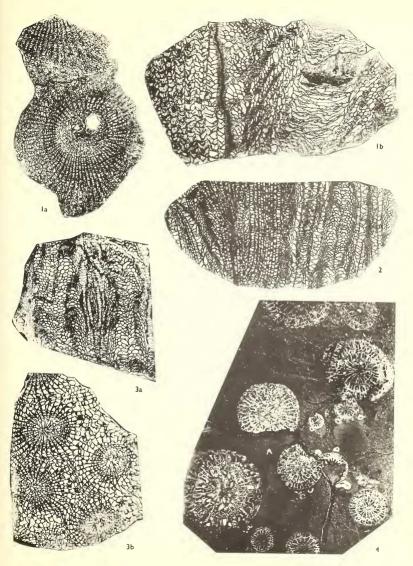
Remarks. SU 6199, from the Loomberah Limestone of Tamworth, N.S.W., placed in B. aperta by Hill (1942c, p. 154, pl. 2, figs. 7a, b), differs from the holotype, and from other specimens from the type horizon, in that its septa are slightly carinate in the

### EXPLANATION OF PLATE 75

Figs. 1 a, b. Hexagonaria approximans cribellum subsp. nov. Topotype SU 13260, loc. Cr–100; transverse (a) and longitudinal (b) sections, ×2; note large diameter. (See also text-fig. 9 a, b.)
Figs. 2, 3. Billingsastraea aperta (Hill). 2, SU 20104, loc. Cr–100; longitudinal section, ×2. 3 a, b,

Figs. 2, 3. *Billingsastraea aperta* (Hill). 2, SU 20104, loc. Cr–100; longitudinal section, ×2. 3 *a*, *b*, Holotype SU 7287, loc. Cr–113, figured Hill (1942*c*, pl. 6, figs. 7 *a*, *b*); longitudinal (*a*) and transverse (*b*) sections, ×2, photographs by courtesy of Prof. D. Hill.

Fig. 4. Peneckiella mesa (Hill). Topotype SU 20103, loc. Gn-20; transverse section, ×4. Specimen collected E. M. Basnett.



STRUSZ, Australian Devonian Rugosa



tabularium, and are less strongly dilated in the dissepimentarium. The Tamworth form may not be conspecific with the Wellington specimens.

*Known localities.* Cr-100, -113 (both in the same biostrome); P-43 (probably the same horizon as the above).

## Billingsastraea speciosa (Chapman 1914)

### Plate 76; text-figs, 10-14

1914 Phillipsastraea speciosa Chapman, p. 306, pl. 49, figs. 10, 11; pl. 50, figs. 12–14. Loyola, Victoria; Gedinnian.

1939a Phillipsastraea speciosa Chapman: Hill, p. 237, pl. 16, figs. 1, 2 only.

1942c Phillipsastraea speciosa Chapman; Hill, p. 183, pl. 6, figs. 8 a, b. Wellington, N.S.W.; Garra Formation, Emsian?

1942c Phillipsastraea sp. Hill, p. 186 (not figured). Wellington, N.S.W.; Garra Formation, Emsian?

1962 Phillipsastrea speciosa Chapman; Philip, p. 176, pl. 24, fig. 6. Tyers R., Victoria; Cooper's Creek Formation, Gedinnian.

Holotype. GSV 2487 (Ferguson Colln.), and thin sections NM 1387, 1388 cut therefrom. Griffith's Quarry, Loyola, near Mansfield, Victoria. The locality was considered by Philip (1960a) to be an equivalent of the Cooper's Creek Formation of the Walhalla basin (south of Mansfield), and therefore early Gedinnian in age.

*Diagnosis.* Astraeoid and thamnsastraeoid, with moderately to strongly fusiform septa, of which the major may reach the axis, or may withdraw almost to the dissepimentarium; tabulae strongly concave.

Description. A large number of specimens have been collected from the Garra Formation; as the species is known from very few specimens at the several Victorian localities, I consider it worth while to describe fully the Garra material.

The coralla are either lamellar, growing on a flat surface of sand, &c., or are broad, low, mushroom-shaped expansions. The largest corallum collected is about 16 cm. across and 6 cm. deep. Only one specimen has an unworn upper surface exposed: on it, the calices are shallow, saucer-shaped, with only slight axial depressions. Adjacent corallites meet in sharp, slightly raised rims.

Thin sections show that individual coralla may be wholly thamnastraeoid, wholly astraeoid, or more usually both. Within one corallum the septa of adjacent corallites may follow several patterns: (1) the septa may terminate within the dissepimentarium, leaving a small gap between their ends; (2) they may meet at a more or less abrupt angle, their ends being coincident or alternate; or (3) they may be completely confluent. Moreover, in a fair proportion of coralla, there may develop between some corallites an outer pseudotheca (Różkowska 1953, see particularly p. 52; this structure is essentially the trabecular wall of Flower 1961, p. 26), formed by the union of the bifurcating ends of septa. This simulates the wall between ceriod corallites (e.g. Hexagonaria), but may be clearly distinguished from that structure in lacking the median dark line (axial plate of Flower 1961) which indicates the presence of an epitheca around the individual corallites. The outer pseudotheca is in fact constructed of the same trabeculae as are the septa. When formed at all in B. speciosa, it is usually very incomplete; consequently in thin section it is generally not possible to measure Dc. A more objective measure is Ts,

the distance between the axes of corallites whose septa abut or are confluent. The data are summarized in the following table of dimensions, and in somewhat more detail under 'Variation'.

Dimensions in mm.

	Dt	n	Ts
Mean	1.76	23.9* 24†	5.12
Minimum	0.9	16	1.5
Maximum	2.8	32	13.8
Lowest mean‡	1.26	18.7* 18†	3.26
Highest mean‡	2.37	27.8* 28†	7.49
No. of readings	374	374	1,050

<sup>\*</sup> Calculated mean; † mean to nearest even number; ‡ means for individual coralla. Readings taken from 12 coralla, from localities Cr-94, -100, -113, P-26, -43.

Most coralla show a fairly small range of *n*, but this range differs markedly from one corallum to another (see 'Variation'). Most septa are greatly dilated, forming a wide stereozone around the tabularium. Outside this stereozone the degree of dilatation varies greatly. Generally the septa are fusiform, but in some coralla they remain dilated throughout the dissepimentarium. This dilatation is often confined to more or less clearly differentiated horizontal layers, which are separated vertically by layers in which the septal dilatation is much reduced. In the dilated layers, the dissepiments may be almost completely suppressed. In the regions of reduced dilatation the septa vary from strongly fusiform, with the stereozone around the tabularium, to only weakly fusiform and almost attenuate, so that there is no stereozone.

In the dissepimentarium the septa may be smooth, but are more often irregularly carinate, the carinae being generally of the zigzag type. The carinae are usually only poorly developed, but on occasions may be very strong; the latter occurs mostly when the septa are fairly thin. Some septa split into two or three parallel thin strands in the dissepimentarium. Finally, there often occur septa which for a short distance become fragmented into discrete trabeculae.

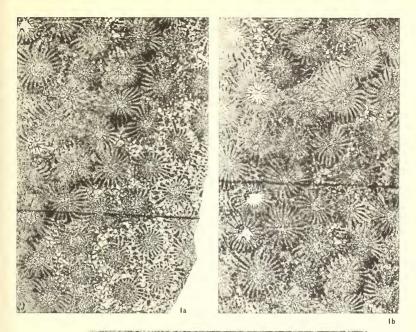
Minor septa barely enter the tabularium. The major septa are more variable; in some cases they extend unequally to the axis, either as continuous plates or as discrete trabeculae; in other cases they withdraw, sometimes to become equal in length to the minor septa. One septum, probably the counter septum, generally extends to the axis, where it is frequently enlarged, forming a rudimentary columella.

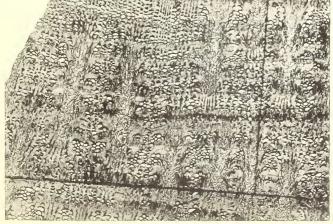
The slender trabeculae are arranged in strong asymmetrical disphylloid fans. The zone of divergence corresponds with the centre of the septal stereozone. In the tabularium the trabeculae are axially inclined at about 45° from the vertical.

The tabularium is narrow. In the coralla measured, Dt varied from 0.9-2.8 mm., but a plot of all Dt showed two peaks at 1.4 mm. and 2.0 mm. (see 'Variation'), and most coralla correspond to one or other of these. The tabulae are moderately sagging, with

#### EXPLANATION OF PLATE 76

Figs. 1 *a–c. Billing sastraea speciosa* (Chapman). SU 13206, loc. Cr–100; (*a*) transverse section showing a region of reduced septal dilatation; (*b*) transverse section of a region of maximum septal dilatation, showing two corallites with shortened major septa; (*c*) longitudinal section; all ×4. Specimen collected by Dr. J. R. Conolly.





lc



rather strongly upturned margins which are supplemented by strongly inclined elongate tabellae.

The dissepimentarium is composed of small globose plates. In a narrow zone around each tabularium, there are two or three series which are very strongly inclined and rather elongate. Outside these, in the zone of maximum septal dilatation, there are one to three series of more or less horizontal dissepiments; beyond these the dissepiments are gently outwardly inclined until midway between tabularia when they are again horizontal.

Ontogeny. The earliest discernible stage in the formation of a corallite occurs generally at the point of intersection of three corallites. Careful inspection of the septa reveals a very small region in which there are six radially arranged plates; some of these may



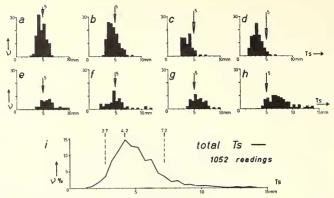
TEXT-FIG. 10. Billingsastraea speciosa (Chapman); transverse section × 5, showing several buds. Traced from photograph of celluloid 'peel'.

be the 'peripheral' ends of septa, others may be carina-like offshoots of septa (text-fig. 10). The next observed stage is a corallite of about  $1\cdot 2$  mm. diameter, with some fourteen septa still not divisible into major and minor. At this stage, the tabularium is distinguishable, Dt = 0.6 mm. Beyond this point, offshoots are not distinguishable from adult corallites. Apparently, therefore, the growth of a bud and the rate of septal insertion are both very rapid. This type of increase is the exact equivalent of the extra-tentacular budding of scleractinians (see Wells, p. F 348, and fig. 250, in Moore 1956).

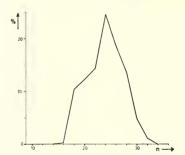
Variation. The three measurable variables in B. speciosa are Dt, n (measured at the margins of the tabularia), and Ts. Only for n and Dt can bivariate analysis be employed using individual readings; for comparison with Ts, mean values of coralla must be compared. It has been found that all three variables show considerable variation from one corallum to another, but relatively little within the one corallum.

Ts (text-fig. 11): this shows the widest range for data from one corallum. Frequency histograms show a broad spread more often than a sharp peak. This spread is even more pronounced in a plot of all data from twelve coralla: the range is from 1·5 mm. to 13·8 mm. overall. Using class intervals of 0·5 mm., the mode is 4·2 mm., and 68 per cent. of the data fall within the interval of classes 2·7–7·2 mm.

n (text-fig. 12): frequency histograms generally show a pronounced peak and a fairly small spread. However, the modes for the 12 coralla measured vary from 18 to 28,



TEXT-Fig. 11. *Billingsastraea speciosa* (Chapman); frequency histograms (*a*–*h*) and percentage frequency curve (*i*) for *Ts. a*, loc. Cr–94; *b*–*d*, loc. Cr–100; *e*, loc. Ge–3; *f*–*l*, loc. P–43. *i*, Total of *Ts* from twelve coralla, localities Cr–94, –100, P–26, –43, Ge–3.



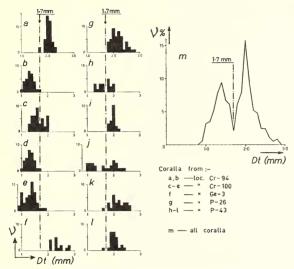
TEXT-FIG. 12. *Billingsastraea speciosa* (Chapman); percentage frequency curve for *n*: 374 readings from twelve coralla, as text-fig. 11.

with a complete range between. A frequency curve for total n is also a fairly tight curve, with a peak at n = 24, and overall range 16–32.

Dt (text-fig. 13): this provides the most interesting frequency distribution. Individual histograms vary considerably both in position and spread. However, a curve for total Dt is distinctly bimodal, modes 1·4 mm. and 2·0 mm., with a sharp low at 1·7 mm. Examination of the histograms in the light of this curve shows that only three of the twelve coralla have modes near 1·7 mm., and of these two also show a very wide spread

of data. Most coralla fall clearly to one or other side of 1.7 mm., and in no one of these coralla do more than 4 per cent. of the measurements fall on the other side of 1.7 mm. from the mode for that corallum.

The plot of n against Dt (text-fig. 14) for all data reflects this dichotomy in Dt, but individual plots give a very wide spread in all directions. The correlation, while not close,



TEXT-FIG. 13. Billingsastraea speciosa (Chapman); frequency histograms (a–l) and percentage frequency curve (m) for Dt.

is enough to suggest that correlation would be obtained for individual coralla by measuring a large number of corallites.

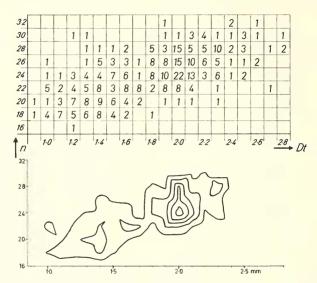
The dichotomy in *Dt* might suggest the possibility of dividing the species into two formae on this basis; unfortunately this is not possible, as several coralla cannot easily be placed on one side or the other of the dividing line.

Comparison. The Garra specimens, apart from the greater degree of variation shown by the much larger sample available, differ from the Victorian specimens principally in the high proportion of tabularia in which there is an elongate, columella-like counter (?) septum. The layered effect of the septal dilatation in the Garra coralla is visible to a lesser degree in the sections of the holotype. The relations of B. speciosa to other species have been noted by Hill (1939).

Known localities. Locs. Cr-94, -100, -111, -113; Ge-3; P-26, -43; BR1 /177. All except

Ge-3 are apparently from the same biostrome, cropping out on either side of a major syncline in the Catombal Group, near Wellington.

*Known range. B. speciosa* is known from the early Gedinnian of Loyola and the Tyers R. in Victoria, and the Emsian or early Couvinian of the Garra Formation.



TEXT-FIG. 14. Billingsastraea speciosa (Chapman); correlation between n and Dt for twelve coralla, as text-fig. 11. Density plot contoured at 1, 2, 3, 4, 5 per cent. of total n.

# Family PHACELLOPHYLLIDAE Wedekind 1922

Diagnosis. Solitary or colonial Rugosa with a well-developed dissepimentarium which includes a vertical series of horseshoe-shaped dissepiments; in this series the horseshoe dissepiments may be replaced by peneckielloid dissepiments. Septa of two orders, composed of one or more radial series of monacanthine trabeculae which are arranged in fans whose zone of divergence coincides with the series of horseshoe dissepiments: the septa are frequently fusiform, and may be carinate. The tabularium may be simple, or composed of tabellae arranged in two or more series.

Remarks. The structure of this family has been discussed in detail on pp. 523-4. Peneckiel-loid dissepiments, a variant form of horseshoe dissepiments, are discussed on p. 555.

## Genus PENECKIELLA Soshkina 1939

1939 Peneckiella Soshkina, p. 23.

1949 *Synaptophyllum* Simpson; Stumm p. 37, non Simpson, 1900. (Subj. synonym, McLaren 1959, pp. 16, 22 q.v. for further discussion on the confusion of these two genera).

1953 Thamnophyllum Penecke 1894 (partim); Różkowska, p. 14.

1958 Peneckiella Soshkina; Schouppé, p. 299. Contains an extensive synonymy.

1959 Peneckiella Soshkina; McLaren, p. 22.

1960 Peneckiella Soshkina; Różkowska, p. 29.

1961 Peneckiella Soshkina; Lenz, p. 505.

Type species. Diphyphyllum minus F. A. Römer 1855, p. 29, pl. 6, figs. 12 a-e. Soshkina 1939, p. 23, incorrectly called the species Peneckiella minima. Minus is the neuter form of minor (m., f.), the comparative of parvus; minimus is the superlative of this word. The type species is therefore Peneckiella minor (Römer).

*Diagnosis.* Fasciculate or cerioid phacellophyllid with septa smooth or weakly carinate, dilated peripherally, or fusiform; with a peripheral series of horseshoe and peneckielloid dissepiments, supplemented by inner, and occasional outer, accessory dissepiments; tabulae generally complete.

Discussion. This genus has been fully discussed recently by Flügel (1956), Schouppé (1958), and McLaren (1959). Flügel described topotypic material, and examined the holotype of Diphyphyllum minus Römer. Unfortunately, he only figured a transverse section, and a diagrammatic longitudinal section. Schouppé described and figured topotypic material. His figures show distinct trabecular fans, a series of horseshoe dissepiments, and occasional dissepiments on either side of this series. These dissepiments are here termed inner and outer accessory dissepiments.

McLaren (1959) discussed the relationship of several American species to the type species of *Peneckiella*, and concluded that they differed from it in lacking horseshoe dissepiments. For the American species he erected the disphyllid genus *Acinophyllum*, which is characterized by carinate septa and only one or two series of normal dissepiments.

Różkowska (1960) described a subspecies of the type species, from the Frasnian of Poland, and, after examining topotypic material from Grund, concluded that the dissepimental structure of *P. minor* (s.l.) is variable. She distinguished four types of dissepiment, which are also recognized herein (text-fig. 15): (i) horseshoe dissepiments sensus stricto; (ii) 'horizontal' dissepiments, usually occurring as what are here termed outer accessory dissepiments; (iii) 'peneckielloid' dissepiments; and (iv) a rare variant of (iii), 'sigmoidal' dissepiments. She found all four types in the one corallite, but more usually only one or two types occur, particularly (i) and (iii) together. The 'horizontal' dissepiments somewhat resemble those in *Thannophylhun*, but are far less uniformly developed. The 'peneckielloid' dissepiments consist of an inner half the same as for horseshoe dissepiments, and an outer half which slopes fairly steeply, straight down to the periphery. The 'sigmoidal' type is a variant of this, closely resembling a combination of horseshoe and horizontal dissepiments, particularly when the sigmoidal outer part touches the surface of a preceding dissepiment before proceeding to the periphery.

As well as occurring in *P. minor kunthi* (Dames) of Różkowska (1960, see figs. 22, 25, 27–29), this variability in dissepimental form can be seen in Schouppé's (1958) figures of *P. minor* (Römer), and also in the specimens of *P. mesa* (Hill) described below.

## Peneckiella mesa (Hill 1942)

Plate 75, fig. 4; Plate 77, figs. 1, 3; Plate 78, fig. 1; text-figs. 16-21

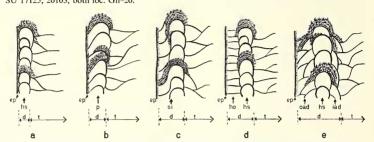
1940a Disphyllum praecox? Hill p. 399 (in text). Wellington, N.S.W.: 'Devonian?'

1942c Disphyllum mesa Hill p. 185, pl. 5, figs. 4, 5. Wellington; Garra Formation, Emsian? 21954a Peneckiella teicherti Hill p. 25, pl. 2, figs. 29 a, b. West Kimberley Ra., W. Aust. (Fitzroy

Basin); 'Atrypa beds', Frasnian.

non 1961 Peneckiella teicherit Hill'; Lenz p. 505, pl. 1, figs. 1, 2. Lower Mackenzie Valley,
Canada; Ramparts Limestone, Givetian.

Holotype. SU 5276 (Pl. 77, fig. 1), loc. Gn-20. Figured Hill 1942c, pl. 5, fig. 4. Other material figured: SU 17125, 20103, both loc. Gn-20.



TEXT-FIG. 15. Dissepimental types found in phacellophyllid species (all diagrammatic, about  $\times$  2 to  $\times$  4).  $a_i$  Horseshoe dissepiments;  $b_i$  peneckielloid dissepiments;  $c_i$  sigmoidal dissepiments;  $a_i$  horseshoe and horizontal dissepiments (as in Thammophyllum Penecke):  $e_i$  horseshoe and accessory dissepiments. ep—epitheca; hs—horseshoe series; p—peneckielloid series; si—sigmoidal series; ho—horizontal series; oad—outer accessory dissepiments; iad—inner accessory dissepiments; id—dissepimentarium; t—tabularium

Diagnosis. Fasciculate Peneckiella with moderately carinate or smooth, thin or fusiform septa, high mesa-shaped tabulae, and dominantly peneckielloid dissepiments.

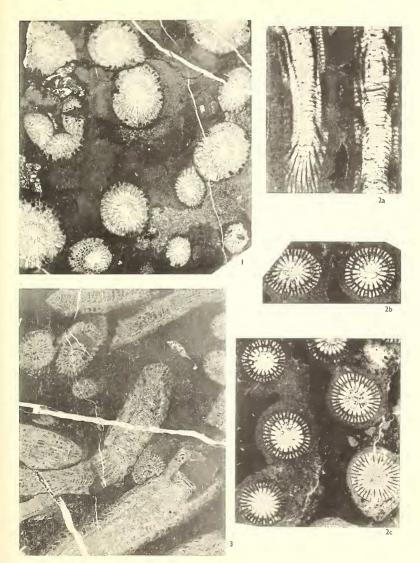
Description. Much additional material has been collected, and so the species is fully re-described.

The corallum is usually phaceloid. The corallites have a thin epitheca, with shallow septal grooves and only slight growth wrinkling. *Dc* is usually about 3–5 mm., but may be over 8 mm. The calix is deep, with vertical walls; the rim is narrow and slightly everted; the floor of the calix consists of a wide mesa-shaped axial boss, surrounded by a deep, narrow concentric trench. There are generally 30–40 septa (see table, p. 557);

## EXPLANATION OF PLATE 77

Figs. 1, 3. *Peneckiella mesa* (Hill). 1, Holotype SU 5276, loc. Gn–20, figured Hill (1942c, pl. 5, fig. 4); transverse section, ×4. 3, Topotype SU 17125, loc. Gn–20; oblique and longitudinal sections—note calix and dissepiments in lowermost corallite (see also text-fig. 16b); ×4.

Figs. 2 a-e. Peneckiella teicherti Hill. Holotype, Univ. W. Aust. 33,515, figured Hill (1955a, pl. 2, fig. 29); Givetian or Frasnian, W. Kimberleys. a, longitudinal and b, c, transverse sections; × 4, photographs by courtesy of Prof. D. Hill.



STRUSZ, Australian Devonian Rugosa



the major are long, unequal, leaving an axial space of  $c. \frac{1}{6} Dc$ ;  $L_2$  is about  $\frac{1}{2} L_1$ , the minor septa normally extended a little way into the tabularium. The septa are weakly to strongly dilated, generally fusiform, with the zone of maximum dilatation a little outside the margin of the tabularium. This dilatation frequently spreads over the surfaces of the innermost dissepiments, and forms an inner stereozone. The septa may also dilate peripherally. Within the dissepimentarium, where the dilatation is slight or moderate, irregular zigzag carinae frequently develop. In the tabularium the septa are thin, and straight or wavy.

e or many.					
Specimen		SU 5276*	SU 17125†	SU 17126†	SU 13145
Dc (mean)	(mm.)	4.1	3.1	3.0	4.0
Dc (max.)	` ′	6.4	5.6	4.7	8.4
Dc (min.)		2.4	1.4	1.8	1.9
No. measurements		20	47	25	70
Dt (mean)	(mm.)	2.5	1.9	1.8	2.3
Dt (max.)		3.9	3.3	2.8	3.2
Dt (min.)		1.5	1.0	1.2	1.3
No. measurements		20	47	25	58
Dt/Dc		0.61	0.61	0.59	0.56
n (mean)		32·5§	31.4	30.8	37-1
		32	32	30	38
n (max.)		40	37	38	46
n (min.)		23	22	26	28
No. measurements		20	33	18	58
n/Dc (mean)	$(mm^{-1})$	0.83	1.12	1.11	0.98
n/Dc (max.)		1.08	1.72	1.44	1.69
n/Dc (min.)		0.48	0.63	0.83	0.60
No. measurements		20	33	18	58
$L_2$ (mean)			0·39 R	0·38 R	0·46 R
$L_2$ (max.)			0.51 R	0.48 R	0.59 R
$L_2$ (min.)			0·21 R	0·24 R	0·25 R
No. measurements			35	25	70

<sup>\*</sup> holotype, loc. Gn-20; † topotypes, loc. Gn-20; ‡ homeotype, loc. Cr-54; § calculated mean; mean to nearest even number of septa.

The septa consist of slender, straight, or slightly curved trabeculae. These are arranged in phacellophylloid fans symmetrical about the axis of the series of horseshoe and peneckielloid dissepiments. The zone of divergence of the fans corresponds to the zone of greatest septal dilatation.

The tabulae are generally complete, rarely incomplete. They are mesa-shaped: the axial parts are flat or gently sagging, while near the dissepimentarium they are turned abruptly down. The periaxial zone is narrow and deep; in it the tabulae, augmented by occasional concave tabellae, are gutter-shaped, with flat or concave floors, high vertical inner walls, and low, upward-slanting outer walls which abut onto the dissepiments. Rare incomplete axial tabulae rest, on all sides, on the edges of the preceding 'mesa'. Dt is c. 0.6 Dc, and the axial zone of the tabularium is about  $\frac{1}{2}$  Dt.

The narrow dissepimentarium consists mainly of a single series of peneckielloid dissepiments, augmented by small horseshoe dissepiments, which in some corallites are